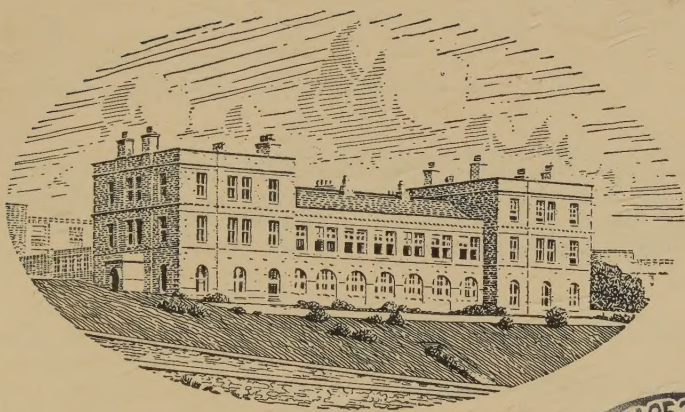


JOURNAL OF THE
MARINE BIOLOGICAL ASSOCIATION
OF THE UNITED KINGDOM

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)
and published by the Cambridge University Press
(Cambridge, and Bentley House, London)
Agents for Canada and India: Macmillan

JOURNAL OF THE
MARINE BIOLOGICAL ASSOCIATION
OF THE UNITED KINGDOM

1880⁶¹



THE PLYMOUTH LABORATORY

VOLUME XXVIII

1949



CAMBRIDGE
AT THE UNIVERSITY PRESS
1949

The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for the accuracy of statements published in this Journal, excepting when those statements are contained in an official report of the Council.

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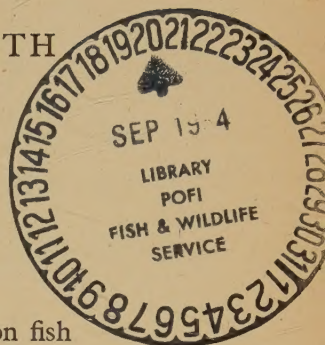
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FURTHER OBSERVATIONS ON FISH GROWTH IN A FERTILIZED SEA LOCH (LOCH CRAIGLIN)

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(Plate I and Text-fig. 1)



In a previous paper (Gross, 1947) an account was given of studies on fish growth in Loch Craiglin under conditions of fertilizer application in 1942/43. From 1944 onwards Drs Marshall and Orr continued to apply fertilizers of different kinds and in varying quantities, and investigated the subsequent growth of phytoplankton (Marshall & Orr, 1948). The sampling of the bottom fauna and of the fish population was much reduced owing to our preoccupation with an experiment carried out in the open Kyle Scotnish (Gross, Raymont, Nutman & Gauld, 1946). However, analysis of the data obtained has established a few interesting points, briefly described here.

GROWTH OF FLOUNDERS FROM 1944 TO 1947

At the end of 1943 the fish population of Loch Craiglin consisted of three stocks of flounders (*Pleuronectes flesus*):

Stock I, transferred to Loch Craiglin in July 1942 when the fish were a few months old (age-group O).

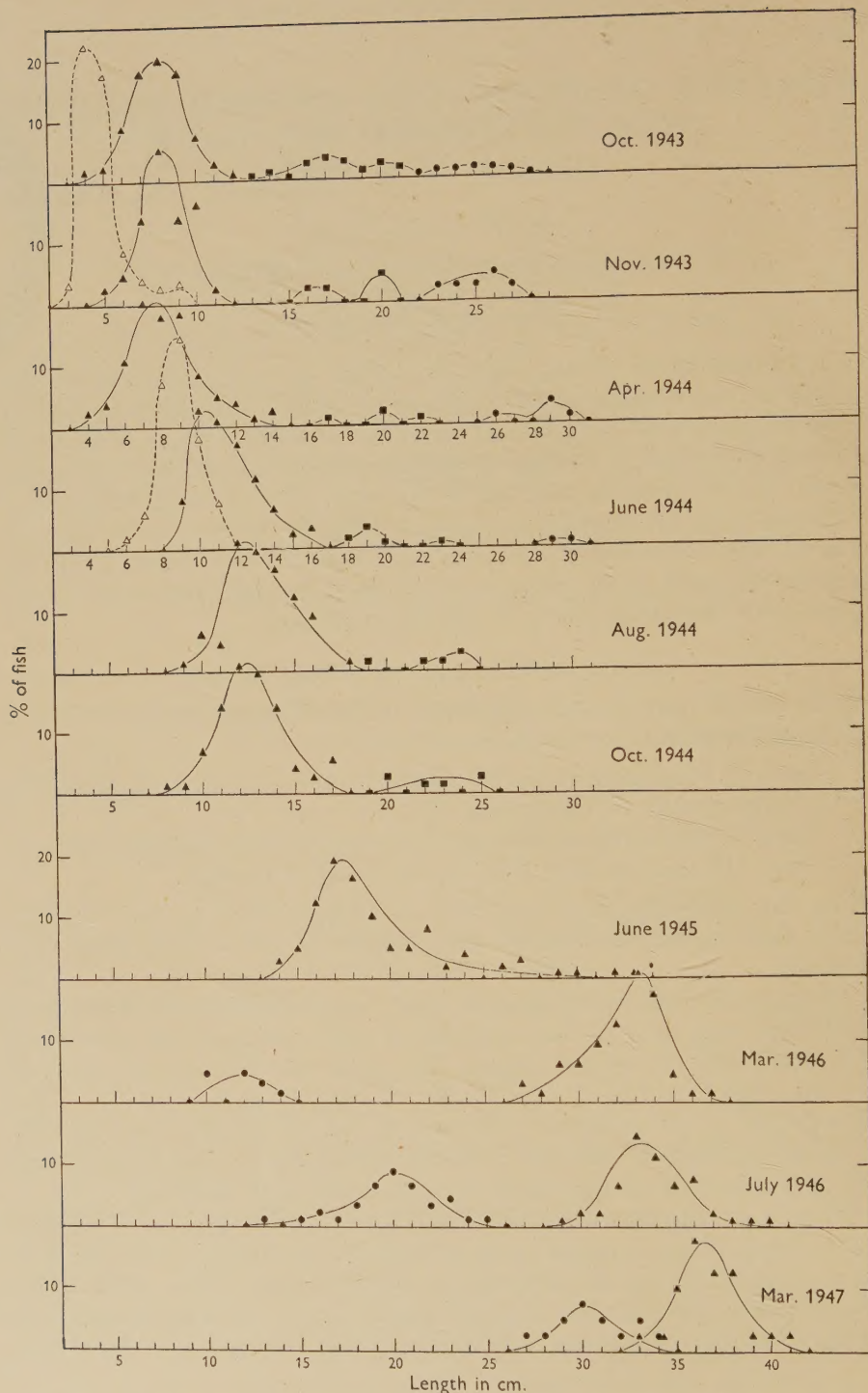
Stock II, transferred in April and May 1943 as 1-year-old fish (Group I).

Stock III, transferred in July 1943 as group-O flounders.

Their size distributions and mean sizes are given in Text-fig. 1 and Table I, which also contain the relevant data concerning the samples taken subsequently.

Comparison of the fish obtained in April 1944 with those from October and November 1943 gives no clear evidence of good winter growth such as was observed during the winter 1942/43. The mean size of stock I increased by 3.3 cm. (13%), and 65 g. (35%), that of stock II by 1.5 cm. (9%), and 19.5 g. (28%), but the numbers involved (6 and 4 respectively) are too small to be of significance. The mean size of the sample of stock III flounders (75 specimens) was almost exactly the same as it was in November.

There is an indication of winter growth of stock III in the shift of the upper limit of range of size to 13 and 14 cm. in April, but an overall increase may have been counteracted by the depredations of cormorants. These were mainly responsible for the reduction of stock I and II, and by selecting the larger fish of stock III may have caused a depression of the average size of population.



Text-fig. 1. The growth of flounders in Loch Craiglin (full lines) and in the estuary of the River Add (broken lines and open triangles). Black triangles refer to stock III, squares to stock II, circles to stock I in 1943/4 and to the native stock in 1946/7.

TABLE I. MEAN SIZE AND CONDITION FACTOR OF FLOUNDERS FROM LOCH CRAIGLIN

Date of capture	Stock III					Stock II					Stock I				
	No.	Age group	Length (cm.)	Weight (g.)	K	No.	Age group	Length (cm.)	Weight (g.)	K	No.	Age group	Length (cm.)	Weight (g.)	K
13: 11/Dec.	215	O	7.9	6.8	1.38	45	I	17.5	66.0	1.23	20	I	25.0	197.3	1.26
14: 11/Dec.	34	O	8.2	7.3	1.33	4	I	18.2	68.7	1.14	6	I	25.4	184.5	1.13
15: 11/Dec.	75	I	8.2	7.5	1.36	4	II	19.7	88.2	1.15	6	II	28.8	259.0	1.08
16: 11/Dec.	114	I	11.6	16.9	1.08	8	II	19.3	72.5	1.01	2	II	29.2	268.5	1.08
17: 11/Dec.	61	I	13.0	23.0	1.05	4	II	22.5	114.2	1.00					
18: 11/Dec.	65	I	12.7	23.6	1.15	6	II	22.4	122.7	1.16					
19: 11/Dec.	98	II	19.2	93.3	1.31										
20: 11/Dec.						'Native stock'									
21: 11/Dec.	54	II	32.3	408.6	1.21	9	O	11.8	20.0	1.22					
22: 11/Dec.	52	III	34.0	463.0	1.18	37	I	20.0	96.1	1.20					
23: 11/Dec.															
24: 11/Dec.	26	III/IV	36.8	580.0	1.16	13	I/II	30.6	353.0	1.23					

The symmetry of the curve relating to the size distribution of the 114 stock III flounders caught in June is even more distorted by the reduction in numbers of the size classes 11–16 cm. than the corresponding curve for the recaptures in April. In contrast to this, the sample of 52 flounders of the same age, caught during the same month in the estuary of the River Add, shows a very symmetrical size distribution around the mean of 8.8 cm., 7.8 g. Therefore the median (12.5 cm.) might be a more accurate estimate of the growth attained by stock III.

Even so, the size of stock III flounders was much smaller than that of stock I at the same age in June 1943 (18.2 cm., 76 g.). The reduction of growth rate was almost certainly due to the deterioration of hydrographic conditions caused by prolonged closure of the dam. The position was aggravated by the distribution on 1 August 1944 of ten times the usual quantity of fertilizers (1344 lb. sodium nitrate and 448 lb. superphosphate), most of which was taken up by, and converted into, sea weed and *Zostera*. The lack of circulation, the consequent drastic reduction in oxygen content and the development of high concentrations of H_2S in the deep water and of very high pH values near the surface, recorded by Marshall & Orr (1948), caused conditions unfavourable for the growth of fish. This continued to be very poor throughout 1944. The growth increment of stock III from June to August was negligible, while from August to October 1944 growth seems to have ceased altogether. The mean value for length was, in fact, a little less in October than in August (Text-fig. 1 and Table I).

Stock I and II specimens became very scarce in 1944. From the few fish (Stock II) obtained it would appear that no growth had taken place from April to June, a slight increase from June to August, and again practically no growth from August to October. The growth increment for the whole year, October 1943 to October 1944, amounted to 4.8 cm., 17 g., in stock III, and

to 4.2 cm., 54 g., in stock II, and was thus of the same order as that recorded for flounders in natural waters.

During the following autumn and winter (1944/45) the sluice gate of the dam was opened to allow interchange of the water with the main loch outside. This led to an improvement in hydrographic conditions and to a striking improvement in fish growth.

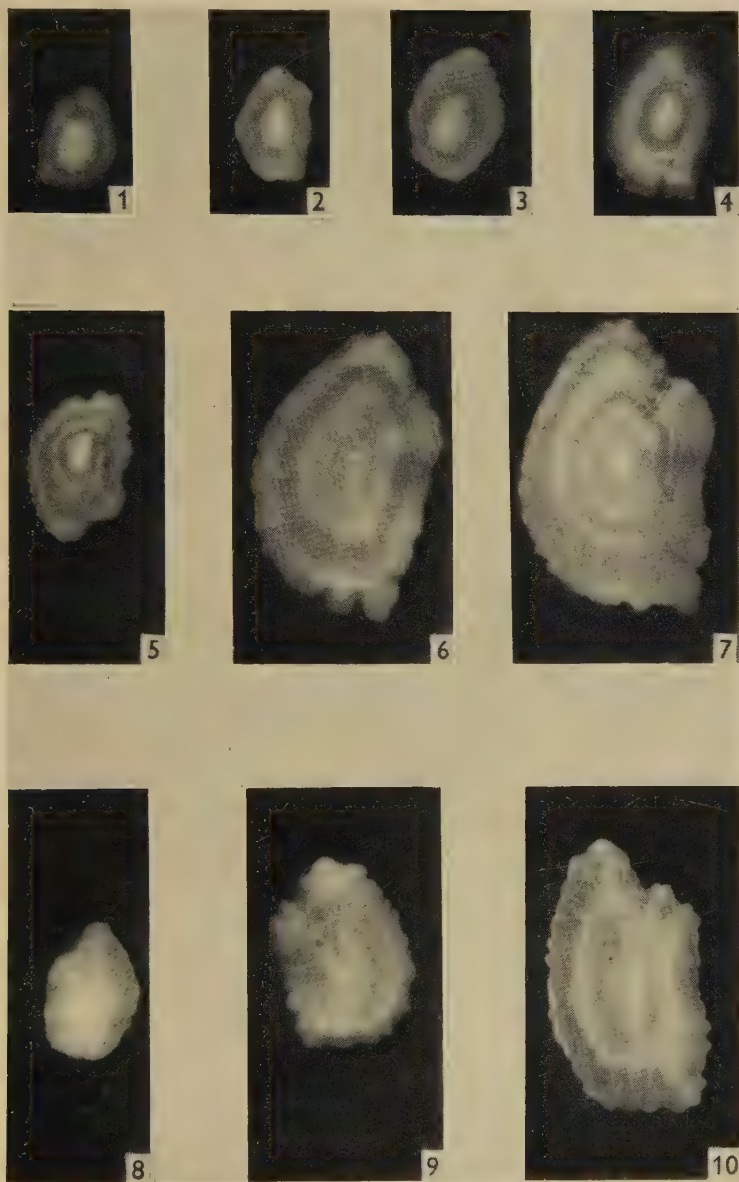
In June 1945 a sample of 99 flounders was obtained (Fig. 1, Table I). Examination of their otoliths, all of which were removed after the fish had been measured and weighed, showed that with the possible exception of one fish (27.4 cm.) all belonged to stock III. Their distribution curve is very asymmetrical. Comparison with the previous curves shows that the growth increment of stock III was greater during the period October 1944 to June 1945 than during the whole of 1944.

The next sample (63 flounders) was caught in March 1946. Of these 54 were 3-year-old stock III specimens. The mode of their size distribution was 33 cm., i.e. 16 cm. greater than in June 1945, a marked improvement over the normal annual growth increment of 4-7 cm. in unfertilized waters. Their growth slowed down again after March 1946. By July of that year they had added very little to their size, and by March/April 1947, at an age of 4 years, their modal class reached 36 cm.

The sample of March 1946 contained 9 group-O flounders of a mean size of 11.8 cm., 20 g. They were obviously 'native' fish which most likely had developed from eggs spawned in Loch Craiglin in 1945. Another sample of 37 of the same native stock, caught the following July, had a mean size of 20.0 cm., 96 g.; and 13 specimens, netted in March/April 1947, had attained an average of 30.6 cm., 353 g., a remarkable growth for 2-year-old flounders.

GROWTH OF OTOLITHS

Examination of the otoliths showed that both the poor growth of the flounders in 1944 and the excellent growth in 1945/46 was clearly recorded by the width of the otolith rings. In 1944, stock III specimens laid on narrow bands similar to fish caught in areas outside Loch Sween (Pl. I, figs. 1-4; see also Gross, 1947), while the bands formed in 1945 were broad and strongly plicated (Pl. I, figs. 6, 7). The extremely wide range of size of stock III flounders caught in June 1945 is illustrated by figs. 5 and 6 (Pl. I) which show otoliths of a small (14.5 cm., 43 g.) and a very large specimen (33.0 cm., 408 g.), both belonging to group II. The very rapid growth of the 'native' flounders in 1946 and 1947, illustrated by three otoliths (Pl. I, figs. 8-10), represents a marked contrast to that of stock III in 1944 (Pl. I, figs. 1-4).



Otoliths of flounders from Loch Craiglin. Magnification of all figures $\times 5.5$.

- Fig. 1. Group O; caught on 16. x. 43; size 10.1 cm., 11 g.
 Fig. 2. Group I; caught on 10. iv. 44; size 10.8 cm., 14 g.
 Fig. 3. Group I; caught on 8. iv. 44; size 13.5 cm., 28 g.
 Fig. 4. Group I; caught on 11. x. 44; size 17.1 cm., 59 g.
 Fig. 5. Group II; caught on 5. vi. 45; size 14.5 cm., 43 g.
 Fig. 6. Group II; caught on 4. vi. 45; size 33.0 cm., 408 g.
 Fig. 7. Group II; caught on 15. iii. 46; size 32.2 cm., 354 g.
 Fig. 8. Group O; caught on 20. iii. 46; size 12.9 cm., 27 g.
 Fig. 9. Group I; caught on 8. vii. 46; size 23.4 cm., 145 g.
 Fig. 10. Group I; caught on 28. iii. 47; size 32.9 cm., 457 g.

CONDITION FACTOR

Comparison of the relation between length and weight of the flounders, expressed by the condition factor (Table I, K ; see also Gross, 1947) reflects the unfavourable conditions for fish growth in 1944, especially during the summer. Condition factors were as low as 1.05 and 1.08 in June and August, rising to 1.15 in October. The condition factor of stocks I and II was very low throughout 1944. In 1945 rapid growth was accompanied by a high condition factor (1.31 in June 1945). It dropped to 1.21 in March 1946, to 1.18 in July 1946, and to 1.16 in March/April 1947. This last, relatively low value may have been correlated with the circumstance that the fish were ripe and may have begun spawning before they were caught. The native stock possessed a fairly high condition factor (1.2–1.23) in all three samples caught.

SEXUAL MATURITY OF THE FLOUNDERS

Of the 52 3-year-old stock III flounders obtained in March 1946 all but 3 females were fully mature: all males and some females were 'running ripe', and while the rest possessed fully developed ovaries the eggs did not run out freely when the animals were stripped. The 4-year-old stock III flounders caught in March/April 1947 (11 females and 15 males) were all mature, 3 of the females spent. Of the 13 'native' fish, just 2 years old, 12 were males, and 11 of these were fully mature, 1 immature, and 1 was an immature female. Thus the onset of maturity occurred in males at the age of 2 years, in females at the age of 3.

DISCUSSION

The observations recorded above represent a postscript to those described and discussed in a previous paper (Gross, 1947) which must be taken into consideration in assessing the growth rate of flounders in manured water as compared with that in natural conditions. The new data are instructive from the point of view of judging the effects of different factors on the growth of flounders. It has been recorded (Marshall, 1947) that a very heavy growth of phytoplankton took place in Loch Craiglin in the spring of 1944, but this did not lead to an improvement in fish growth. The distribution of ten times the usual quantity of fertilizers in August 1944 brought about a disproportionately small increase of phytoplankton crop and marked the beginning of a period of complete cessation of fish growth. There is every reason to believe that fish growth did not slow down and finally stop owing to shortage of food, but because of extremely bad hydrographic conditions consequent upon the prolonged closure of the dam. The growth increment of stock III flounders for the year October 1943 to October 1944 amounted to merely 4.8 cm., 16.8 g., which is approximately the annual growth increment of flounders in natural waters.

In 1945, after several months of interchange of water through the open sluice, the chemical and physical conditions in the loch improved, and during the period October 1944 to March 1946 the flounders increased by 19.6 cm. (155%) in length and by 385 g. (1660%) in weight, a very marked improvement on any records of marine fish growth in natural waters. Fertilizers were applied only on four occasions during that year, all during the period February-April 1945, 23 lb. N and 3.4 lb. P being added each time. During 1946, fertilizers were applied on two occasions only (superphosphate along with ammonium chloride on one occasion and urea on the other); these had little effect on phytoplankton density (Marshall & Orr, 1948). During the same year the growth of stock III flounders slowed down considerably. The growth increment from March 1946 to March 1947 amounted to only 4.5 cm., 171 g. On the other hand, the 'native' stock increased during the same period by 18.8 cm., 333 g., to 30.6 cm., 353 g., at an age of 2 years. They were thus about 5 cm. longer, and 150 g. heavier than stock I flounders at the same age. The slower growth of stock III specimens during 1946 may have been due to their sexual maturation and subsequent spawning, and perhaps also to the predominance of *Hydrobia*, not taken readily by flounders, and the relative scarcity of *Cardium* and chironomid larvae, favoured by these fish, and especially perhaps by larger specimens.

The new data, in conjunction with the results obtained in 1942/43, lead to the conclusion that distribution of fertilizers can bring about a very great increase in the growth rate of flounders, provided the hydrographic conditions are favourable. Though the last application of fertilizers was made in January 1946, the fertility level represented by the growth of fish remained high throughout 1946 and 1947, and, though declining, will probably remain above the pre-fertilization level for some years owing to the regeneration of nutrients locked up in great accumulations of organic material, remains of previous fertilizations.

There seem to be very few records concerning the relation of size, age and sexual development of fish. If maturity is correlated with a certain age and not with size, fish which grow more rapidly under conditions of fertilization would reach a considerable size, well above the minimum limit for marketing, before spawning. The maintenance of fish stocks, on the other hand, depends to a great extent on the size of the breeding stock, i.e. on the number of fish which have spawned before they were caught.

From the few published data it would appear that flounders, like plaice, normally mature at the age of 4-5 years, and that males reach maturity a year earlier than females. Kändler (1932) found that, in 1931, flounders of the Oder Bank reached maturity one year earlier than in 1925, the majority of females at the end of the fourth year, some males already at the end of the third year. He correlates the acceleration of maturity with an increase in growth rate from 1925 to 1931, due to thinning out of stock. In the Danzig area and in the central parts of the Baltic the flounders reached maturity at

a higher age, males at 5, females at 6, and the size of the various groups was markedly smaller (Kändler, 1932). Molander (1932) investigated the flounder stocks off the Swedish coast in 1930/31 and found no spawning females of lesser size than 22 cm. and younger than group IV. Males were ripe at a length of 18–22 cm. and belonged to group III. In previous years spawning males, 13–15 cm. long, were also recorded. These presumably were also group-III flounders which had grown more slowly than those caught in 1930/31.

The fish obtained in Loch Craiglin also provide some useful evidence concerning the relationship between size, age and maturity. In March 1946 the great majority of 3-year-olds, both males and females, were fully ripe, and in March 1947 2-year-old males were ready for spawning. Only one 2-year-old female was obtained which was immature. Thus the males, at any rate, under conditions of fertilization and greater abundance of food, have matured at an age of 2 years. The data suggest, therefore, that sexual development in flounders goes with size rather than with age.

SUMMARY

Flounders grew much more slowly in 1944 than during the previous 2 years. From October 1943 to October 1944 their mean size increased from 7.9 cm., 6.8 g., to 12.7 cm., 23.6 g., an increment which was if anything smaller than under normal conditions. The reason for the reduction in growth rate is attributed to the increasingly unfavourable hydrographic conditions resulting from the prolonged closure of the dam, in particular to the high H_2S concentration, the high pH and the low oxygen concentration of the water.

In the autumn of 1944 the sluice gate of the dam was opened for several months. In 1945/46 the growth of stock III flounders was very rapid. They reached a mean size of 32.3 cm., 409 g., in March 1946 and 36.8 cm., 580 g., in March/April 1947. Native flounders reached a mean size of 30.6 cm., 353 g., in 2 years.

The poor growth in 1944 was reflected in narrow bands laid on by the otoliths and in low condition factors (1.05–1.15), the subsequent great improvement in growth rate was correlated with broad rings and high condition factors (1.31–1.16 in stock III, 1.2–1.23 in the native stock).

In March 1946 most females and all males were ripe at an age of 3 years. In March/April 1947 10 males were fully ripe at 2 years of age. These observations, in conjunction with those recorded by Kändler (1932), suggest that sexual maturity is correlated with size and not with age.

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FURTHER OBSERVATIONS ON CHANGES IN THE BOTTOM FAUNA OF A FERTILIZED SEA LOCH

By J. E. G. Raymont
University College, Southampton

(Text-fig. 1)

INTRODUCTION

An account has already been given (Orr, 1947; Marshall, 1947; Marshall & Orr, 1948; Gross, 1947; Raymont, 1947) of the changes resulting from the application of fertilizers to a small sea loch (Loch Craiglin) during 1942 and 1943. Remarkable increases in plankton production were observed, and these were followed by a considerable increase in the bottom fauna, the most obvious rise occurring during the second summer of fertilization. All the more important species of the bottom fauna exhibited increases and an average density of some 16,000 animals/m.² was reached during August 1943, as compared with less than 5000 in the previous summer. The population declined with the approach of winter, but the average winter population for 1943-44 of a little over 7000 animals/m.² showed an increase of 300 % over the 1942 corresponding winter population (Raymont, 1947).

The last regular samplings were made in February 1944, but a further series was taken in May. Thereafter, as heavy applications of fertilizers had been made throughout the summer of 1944 and again during the early spring of 1945 (Marshall & Orr, 1948), the series of grab samples was repeated every summer and continued until September 1947 in order to investigate the long-term effects of accumulated fertilizers on the bottom population.

METHODS

The samples were taken at the same stations in the loch as in 1942 and 1943, except that Station VI was abandoned at the beginning of 1944. The bottom fauna there was very similar both in species and density to that at St. VII. A few samples were taken at a new station (St. VIII) sited fairly close to the north-west shore near the edge of the sparsely populated zone (see Raymont, 1947), as it was considered that the changes in that part of the loch had not been closely followed in the early work.

The samples were taken with the modified Petersen grab removing $\frac{1}{16}$ th m.² of the bottom, the material was washed through a 1 mm. sieve, and all the animals were preserved and counted later.¹ The results are therefore strictly comparable with those obtained in 1942 and 1943.

¹ I wish to thank the Department of Scientific and Industrial Research for a grant in respect of an assistant for 1946-47.

CHANGES IN THE BOTTOM POPULATION

The density of the bottom fauna in May 1944, as revealed by the grab samples, showed an unexpected drop as compared with the previous winter value. Some increase with spring reproduction might have been expected by May, but on the contrary, Sts. III-V and VII all showed declines, the population at

TABLE I. THE BOTTOM FAUNA OF FIVE STATIONS, EXPRESSED IN NUMBERS OF ANIMALS/M.², SHOWING CHANGES FROM SUMMER 1943 TO SUMMER 1947

	Aug. 1943	Feb. 1944	May 1944	Aug. 1944	Sept. 1945	Sept. 1947
Station II						
Chironomids	8,128	—	360	1,520	496	—
<i>Hydrobia</i>	5,888	1,360	1,520	2,096	2,528	7,632
<i>Cardium</i>	592	—	—	—	64	—
Crustacea	32	—	—	—	80	—
Other organisms	160	—	—	—	—	—
Totals	14,800	1,360	1,880	3,616	3,168	7,632
Station III						
Chironomids	11,584	—	944	7,024	9,152	40
<i>Hydrobia</i>	3,904	5,664	800	3,744	9,936	5,320
<i>Cardium</i>	6,528	—	—	272	2,224	—
Crustacea	128	—	—	32	1,152	—
Other organisms	160	—	—	288	—	—
Totals	22,304	5,664	1,744	11,360	22,464	5,360
Station IV						
Chironomids	7,568	10,816	6,896	3,504	23,568	1,496
<i>Hydrobia</i>	2,304	1,984	1,384	1,648	14,704	8,848
<i>Cardium</i>	8,624	16	8	—	2,000	48
Crustacea	1,776	1,264	16	16	2,000	216
Other organisms	736	6,992	2,856	112	80	64
Totals	21,008	21,072	11,160	5,280	42,352	10,672
Station V						
Chironomids	11,952	2,256	4,544	560	12,176	2,488
<i>Hydrobia</i>	7,280	6,016	3,032	2,944	31,280	8,704
<i>Cardium</i>	2,704	—	8	144	3,296	—
Crustacea	48	80	—	48	272	8
Other organisms	80	592	400	—	48	—
Totals	22,064	8,944	7,984	3,696	47,072	11,200
Station VII						
Chironomids	15,216	4,176	4,216	768	14,544	2,280
<i>Hydrobia</i>	4,656	4,560	4,288	1,168	20,608	27,048
<i>Cardium</i>	3,680	—	128	16	3,536	48
Crustacea	—	—	16	32	464	96
Other organisms	608	1,008	448	—	592	192
Totals	24,160	9,744	9,096	1,984	39,744	29,664

St. IV being almost halved (Table I). By August, chironomid larvae and *Hydrobia ulvae* did show some increase at Sts. II and III, but the density of individual species and the total population at these stations was far below the 1943 summer level: at St. II the total population was only one-fourth, at St. III only one-half of that of the previous year. Even more striking were

the changes in the region of the usually rich stations (Sts. IV, V and VII). The sharp decline continued there from May to August, when only 2000–5000 animals/m.² were present along this normally rich zone. This density may be compared with 21,000–28,000 in the same region in the previous August.

The average population of Loch Craiglin, calculated from the populations at Sts. I–V (i.e. assuming as before that each station represents one-fifth of the population of the loch), showed a decline from 16,000/m.² in August 1943 to under 5000 in 1944 (Table 2). The decrease affected almost every species of the bottom fauna, and in particular the normal summer spatfall of *Cardium*, and the rise in *Idothea* and *Gammarus* practically failed to occur.

Considerable deoxygenation occurred during 1944. Therefore from September the dam separating Loch Craiglin from Loch Sween was left fully open for several months so that a fairly complete exchange of sea water could take place. Early in 1945, when healthy conditions had been fully re-established, the dam was closed and several fertilizations were made which were followed by good phytoplankton increases (Marshall & Orr, 1948).

TABLE II. THE AVERAGE BOTTOM POPULATION OF LOCH CRAIGLIN FROM 1942 TO 1947, EXPRESSED IN NUMBER OF ANIMALS/M.²; CALCULATED FROM GRAB SAMPLES TAKEN AT STS. I–V.

	Sept. 1942	Aug. 1943	May 1944	Aug. 1944	Sept. 1945	Sept. 1947
Chironomids	3,302	7,850	2,549	2,522	9,078	806
<i>Hydrobia</i>	920	3,875	1,347	2,086	11,693	6,578
<i>Cardium</i>	62	3,690	3	83	1,517	10
Crustacea	97	397	3	19	701	45
Other organisms	385	227	651	80	25	14
Totals	4,766	16,039	4,554	4,790	23,014	7,451

A full series of grab samples in September 1945 revealed a general and great rise in population density. The average calculated from the densities of Sts. I–V reached 23,000 animals/m.² which is nearly 50 % higher than even the peak population obtained in the summer of 1943. Further, all the more important species of the bottom fauna (chironomid larvae, *Hydrobia*, *Cardium*) responded, the average density of *Hydrobia* being three times the population two years before (Table II). Along the whole rich east shore there was an average population of well over 40,000 animals/m.² (Table I, Sts. IV, V and VII): this was nearly double the population of 1943 and represented the highest density recorded up to that time in Loch Craiglin.

There is fairly strong evidence that the high productivity was maintained throughout 1946. In September of that year a further series of grabs was taken, but unfortunately a number were lost during transport to the laboratory. Reliable counts can be given only for Sts. I, V, VII and VIII (Table III). At Sts. V and VII the total population of chironomid larvae, *Hydrobia* and *Cardium* (the number of other organisms was probably very small), was 29,000 and 52,000 respectively. St. V had thus declined from the 1945 peak

value, but St. VII had increased again and the population was the highest ever recorded at any time. While it is impossible to calculate from these few samples an average population for Loch Craiglin for the summer of 1946, it seems fairly safe to assume that the general population did not decline very obviously during that year.

Table III shows that for the first time since 1942, St. I had a significant population composed almost entirely of *Hydrobia*. Also at Sts. V, VII and VIII, more than 90 % of the bottom fauna (at St. VIII practically 100 %) was made up of *Hydrobia*. Already in 1945 it was clear that *Hydrobia* had increased far more relatively than either chironomid larvae or *Cardium*, but the rise in *Hydrobia* in 1946 was far more striking.

A final series of grabs was taken in the following summer. The population at St. V was only 11,000 as compared with 29,000/m.² in 1946. At St. VII there was a similar drop from 52,000 to 30,000/m.² Comparable figures are not available for the other stations owing to the loss of samples in 1946, but

TABLE III. THE BOTTOM FAUNA OF FOUR STATIONS IN SEPTEMBER 1946, EXPRESSED IN NUMBERS OF ANIMALS/M.²

	St. I	St. V	St. VII	St. VIII
Chironomids	16	2,128	1,040	32
<i>Hydrobia</i>	448	27,264	50,592	20,288
<i>Cardium</i>	—	32	96	—
Other organisms	?	?	?	?
Totals	464	29,424	51,728	20,320

we may compare the populations at these stations with the 1945 values. Thus St. III dropped from 22,000 to only 5000, and at St. IV there was a similar decline to approximately one-quarter of the 1945 population—from 42,000 to 11,000/m.² (Table I).

Station II was, however, exceptional, showing a rise in population from 3000 in 1945 to over 7000/m.² in 1947 (Table I). At St. I also the population rose to some 2400 animals in 1947, all consisting of *Hydrobia*. The actual density is somewhat doubtful, as the two samples taken at St. I differed considerably when counted. Probably one grab struck the side of the deep pit round St. I and gave the higher count. Nevertheless, what is significant, is the fact that the recolonization of the azoic zone round St. I which was fore-shadowed in 1946 continued throughout 1947.

Excepting Sts. I and II, there was a very sharp decline in 1947 from the peak 1945 levels and the average population for Loch Craiglin, calculated from the densities at Sts. I-V, decreased to about one-third of the 1945 density—from 23,000 to 7500/m.² (Table II).

So far only the changes in numbers of the bottom fauna have been given. It is clear, however, that from the point of view of fish food it is the *weight* of the organic matter in the bottom fauna (i.e. excluding the shells and other indigestible matter) rather than numbers which is really significant.

The dry organic weights of the bottom fauna (i.e. dry weight less shell) have therefore been calculated approximately for the years 1944 to 1947. The method used previously (Raymont, 1947) has again been employed so that the data for earlier years are comparable. The average dry weight of all the commoner members of the bottom fauna was determined and the average numbers of bottom fauna given in Table II have been converted into dry weights. The results are shown in Table IV.

In the summer of 1942 the average dry weight of bottom fauna in Loch Craiglin was only 3 g./m.² The weight fell to a minimum of 1 g./m.² during the following winter, but rose rapidly during the summer reaching over 9 g./m.² in August 1943 when a high density of some 16,000 animals/m.² was present. This higher weight was maintained during autumn, but by February 1944 the average weight was reduced to 5 g./m.² By May 1944 the dry weight had fallen further to below 3 g./m.², and in August there was only a very slight recovery to 3.5 g./m.²

TABLE IV. THE AVERAGE DRY WEIGHT, IN G./M.², OF THE BOTTOM FAUNA OF LOCH CRAIGLIN (CALCULATED FROM THE NUMBERS OF ORGANISMS AT STS. I-V, WEIGHT OF SHELLS OF MOLLUSCA EXCLUDED).

	Feb. 1944	May 1944	Aug. 1944	Sept. 1945	Sept. 1947
Chironomids	1.3	1.3	1.3	4.5	0.4
<i>Hydrobia</i>	3.1	1.4	2.2	12.1	6.8
<i>Cardium</i>	—	—	0.1	2.2	0.1
Crustacea	0.3	—	—	0.8	—
Other organisms	0.2	0.1	—	—	0.2
Totals	4.9	2.8	3.6	19.6	7.5

The change in dry weight between 1944 and 1945 is striking: by September 1945 the average dry weight of the bottom fauna was between 19 and 20 g./m.² Of the few counts made in 1946 the large numbers of *Hydrobia* recorded would suggest that a considerable weight of bottom fauna was present at that time. By September 1947, however, the dry weight had fallen markedly to an average of 7.5 g./m.²

DISCUSSION

It is clear from Tables I and II that, with the exception of the deoxygenated pit round St. I, there was a very marked and general rise in the density of bottom fauna over the whole of Loch Craiglin from the summer of 1942 to summer 1943, but that every station experienced an equally obvious drop in population in the following summer (August 1944).

It might be claimed that, since the 1942 and 1944 summer populations are approximately equal and that fertilization was practised over all three years, the very high population of 1943 was not due mainly to a general increase in the amount of food, consequent upon fertilization, but was merely due to annual variations caused by other factors. This is unlikely in view of the fact

that *all* the important bottom fauna species in Loch Craiglin showed marked increases in 1943. Nevertheless, it is true that the sharp decline in 1944 occurred in spite of a peak production of phytoplankton in the early months of that year, and despite the fact that the loch was still very rich in nitrates and phosphates which would indicate a very high *potential* productivity. But it must be admitted that however high the potential productivity of a body of water may be, factors other than the amount of food available may limit the actual production. It is possible, therefore, that the drop in bottom fauna density in the spring and summer of 1944 was due to some deleterious factor operating then but not during previous years, and that in the absence of this factor the population in 1944 would have been as high (or even higher) as in the previous year. That some depressing factor was acting seemed likely also from the observations by Gross (1949) that the growth of flounders in Loch Craiglin during the spring and summer of 1944 fell off very considerably.

From the autumn of 1943 the deoxygenation of the deep pit around St. I became progressively more marked, and throughout the spring and summer of 1944, there was a considerable production of hydrogen sulphide. It is believed that these unhealthy conditions spread out from this area during 1944, and, in contrast to previous years, affected a large proportion of the loch. This deoxygenation was caused mainly by the decay of exceptionally heavy growths of *Zostera* and sea weeds. These rich growths resulted from excessively heavy fertilizations in 1944, one summer fertilization, for example, consisting of ten times the normal quantity of fertilizers applied (Marshall & Orr, 1948).

The widespread deoxygenation even so was probably confined mainly to the mud surface. Although, therefore, a large part of the bottom fauna died, some animals living normally well above the bottom survived. This may account for the fact that *Hydrobia* showed a smaller drop in population from 1943 to 1944 than any other species (cf. Fig. 1), for *Hydrobia* typically lives on the weed in Loch Craiglin. On the other hand, chironomid larvae which are known to be able to withstand very low oxygen concentrations were very greatly reduced in number, but these were living in the mud surface.

If deoxygenation really did limit the production in 1944, the re-establishment of 'healthy' conditions should have led to an increased productivity. It is very significant therefore that following a full exchange of sea water later in 1944 between Loch Craiglin and Loch Sween, fertilization in the next spring produced very marked plankton increases, and further that the bottom fauna density rose very rapidly and generally over the loch to values higher than any previously recorded. Along the eastern side of Loch Craiglin the average population reached more than 40,000 animals/m.² The average population in September 1945 was five times the average density in 1942 and 1944, and nearly 50 % higher than that of 1943. The great increase in 1945 may be attributed to a general raising of the level of productivity by fertilization and

this rise in productivity is reflected also in the excellent growth of flatfish (Gross, 1949) over the same period.

Although these flatfish continued to feed heavily upon the bottom fauna, and despite the fact that only a very little fertilizer was applied to the loch during 1946, there is some evidence for the view that the bottom fauna productivity was maintained at a fairly high level over the summer of 1946.



Fig. 1. Variation in the average density and composition of the bottom fauna in Loch Craiglin for the summers 1942-47, calculated from the populations at Sts. I-V. (Samples from all stations were not available for 1946.)

Thus, of the few records available, St. V showed a decline but St. VII an equally marked increase. The population at St. VII ($52,000/m.^2$) was indeed the highest recorded during the course of the investigation.

The fact that St. I also showed a population of some $400-500$ *Hydrobia*/ $m.^2$ in the summer of 1946 is strong evidence for the view that the good hydrographic conditions established in 1945 continued throughout the following year. No animals of any kind were recorded around St. I from the summer of 1942 to 1945 owing to the deoxygenation of that region, but in 1946 *Hydrobia* was able to maintain itself.

By 1947, the population at St. I, still consisting entirely of *Hydrobia*, had increased five times. Thus we may conclude that good oxygenation and other favourable hydrographic factors, apart from dissolved nutrients, existed throughout 1947 also. In support of this conclusion, none of the samples taken in Loch Craiglin in 1947 smelled strongly of H_2S . Further, St. II, which bordered the previously deoxygenated zone and showed a very marked reduction in population in 1944 when oxygen was low, actually showed a rise in population in 1947.

Yet, although the general hydrographic conditions in 1947 would appear to have been favourable, the bottom fauna numbers in general fell very sharply. The average density dropped from 23,000/m.² in 1945 to 7500 in 1947, and along the rich eastern shore the density fell from about 40,000/m.² to approximately 14,000.

The last application of fertilizers to Loch Craiglin was made in spring 1945, except for a very little added in January 1946. Thus by the summer of 1947 some two and a half years had elapsed without any significant addition of fertilizers. It is suggested that the lowered bottom fauna density in 1947 is therefore correlated with a general lowering in the amount of nutrients available.

The decline did not affect all members of the bottom fauna to the same extent. The *Cardium* and crustacean populations were extremely small in 1947 as compared with 1945; in fact the expected summer spatfall of *Cardium* apparently failed altogether (see Tables I and II). The average density of chironomid larvae also declined very sharply: from 9000 to only 800/m.², this population being only one-quarter of even the 1942 summer population. On the other hand, the density of *Hydrobia* fell only to about a half of the 1945 peak density. Indeed at Sts. I-III the whole population in 1947 was virtually *Hydrobia* and at the richer stations (IV, V and VII) this species comprised from 75 to 90 % of the whole bottom fauna.

In 1945 *Hydrobia*, for the first time during the course of the investigation, became the dominant organism of the bottom fauna in Loch Craiglin (see Fig. 1). Analysis of the few samples in 1946 indicated that its dominance was increasing, and this apparently continued throughout 1947. It is believed that the rise in *Hydrobia* originally was due to its ability to avoid the low O_2 tensions near the bottom. But probably from 1946 to 1947, when with somewhat lowered productivity a stronger competition existed between the species of the bottom fauna for the food available, the large population of *Hydrobia* progressively crushed out its competitors.

There is also the differential grazing effect of the bottom fauna by the flounders. In Loch Craiglin chironomid larvae and *Cardium* were always favourite foods, but *Hydrobia* was not taken so readily. The very great reduction in chironomids in 1947 was probably due to intensive grazing out-stripping production. *Cardium*, as well as being eaten, was also killed off to a considerable extent in Loch Craiglin by winter frosts (cf. Raymont, 1947).

Thus by September 1947 the density of *Hydrobia* was eight times that of chironomid larvae, and the total density of all other animals was quite insignificant.

Although fertilization of Loch Craiglin began in 1942, peak values of the bottom fauna were achieved only in 1945. Perhaps similar high values would have been reached in 1944 had healthy conditions existed then. But it would seem that when fertilizers continue to be added, at least 2-3 years are necessary to achieve anything approaching maximum productivity from the bottom fauna. Similar conclusions have been drawn from other fertilization experiments in an open sea loch (Raymont, 1948). Whether higher densities would have been obtained had fertilization continued it is impossible to tell. We can say that after more than two years' lack of fertilization there would appear to be a real falling off in bottom productivity. But even then, a fairly high productivity, certainly greater than pre-fertilization values, is still maintained. Table II shows that the average bottom density in 1947 was 7500/m.² as compared with less than 5000/m.² in 1942 when some beneficial effect of fertilization had probably already been experienced.

Even clearer, however, is the increase in bottom fauna productivity from 1942 to 1947 if the dry weights are considered. The rise in numbers from 1942 to 1943 was paralleled by a trebling of the average weight of bottom fauna. The decline during the following winter was due mainly to the reduction of chironomid larvae and young *Cardium*. *Hydrobia* was much less affected, probably because it was not eaten very much.

The expected rise in dry weight in the summer of 1944 did not occur; the increase from May to August was only 0.5 g. and the weight of the bottom fauna was then almost identical with that in 1942.

The rise in the summer of 1945 is therefore all the more striking, and the average dry weight of nearly 20 g./m.² recorded in September compares very favourably with the weights of bottom fauna given by Zenkewitch, Brotzky & Idelson (1928) and Petersen (1918) for the rich White Sea and Limfjord regions. Their figures of 20-100 g. and 50 g./m.² represent total *wet* weights, and a reasonable estimation of the dry weights is about 10 % or less, giving thus 2-10 g. and 5 g. respectively. It is true that Zenkewitch *et al.* found some areas with 20-30 g. (dry weight). Loch Craiglin would appear to be almost as rich as this.

By 1945 the weight of bottom fauna in Loch Craiglin indicated that it had become an exceedingly rich feeding ground. The weight was just over double what it was in the summer of 1943, and more than six times the 1942 value (Table IV). On the other hand, the average number of bottom animals in 1945 (23,000/m.²) is only some 45 % greater than that of 1943 (16,000/m.²). The difference lies in the fact that *Hydrobia*, which has a higher dry organic weight than either chironomid or very young *Cardium*, made a much greater contribution to the bottom fauna in 1945. Of the total average weight of 19.6 g./m.²,

Hydrobia contributed no less than 12 g., chironomid larvae 4.5 g. and *Cardium* only 2.2 g. The weight of *Cardium* seems especially small, but it must be remembered that in Loch Craiglin the vast proportion of *Cardium* were less than 5 mm. long. Thus, in 1945, of an average population of 1520 *Cardium*/m.², some 1260 were less than 5 mm. and only 45 were over 10 mm. in length. The average dry weight of *flesh* in cockles of less than 5 mm. length is very small—approximately only 0.2 mg. per individual.

It has been suggested that by 1947 there was a real and significant fall in productivity in Loch Craiglin. The dry weight in 1947 was somewhat below the 1943 summer value (9 g.), but the difference was not great. On the other hand, the number of organisms in 1947 was less than half the 1943 density. Once again the apparent discrepancy is explained by the fact that *Hydrobia* contributed to a very much greater extent in 1947: 6.8 g./m.² out of the total 7.5 g. is made up by this one species.

The importance of dry-weight determinations is thus clear in these bottom fauna investigations. Although numbers and weight were declining in 1947, by September, some two and a half years after the last significant quantity of fertilizers had been applied, Loch Craiglin was still more than twice as rich in weight of bottom fauna as it was in 1942.

From the summer of 1942 onwards the weight of bottom fauna in Loch Craiglin was made up almost entirely of chironomid larvae, *Hydrobia*, crustacea and *Cardium*. Had a considerable proportion of the cockles been of large size, they would not have been available to relatively small-mouthed fishes such as flounders. Even the very rich feeding grounds investigated by Zenkewitch *et al.* may be only *apparently* rich, since it is uncertain how much of the bottom fauna was edible and available (cf. also Ford, 1925). In Loch Craiglin, however, the vast majority of *Cardium* were very young individuals in any year, and the other common organisms were all readily available. Therefore the weights of bottom fauna given can be regarded truly as the quantities of food available to the feeding fishes.

SUMMARY

An account is given of the further changes in the bottom fauna of a fertilized sea loch (Loch Craiglin) from 1944 to 1947, and the results are compared with those obtained from 1942 to 1944.

The bottom fauna density fell markedly during 1944, despite the addition of very large quantities of fertilizers. Unfavourable hydrographic conditions, especially low oxygen tensions, are considered to be responsible for the decrease.

Densities higher than ever obtained before in Loch Craiglin were found in the summer of 1945 (average of 23,000 animals/m.²), when favourable hydrographic conditions once more existed.

The little evidence available suggests that the high productivity was maintained during 1946, although only a very little fertilizer was added during that year.

By 1947 the average density of bottom fauna had fallen to only 7500 animals/m.² and it is suggested that this drop was correlated with less nutrients being available, since no fertilizers were added after January 1946.

Hydrobia ulvae became progressively more important from 1944 onwards, and was the dominant member of the bottom fauna from 1945. Reasons are advanced for the progressive rise in numbers of this species.

The average dry weight of flesh of the bottom fauna rose from 3 g./m.² in 1942 to 9 g./m.² in the summer of 1943. It fell to 3.5 g. in 1944, rose to 19.5 g. in 1945 but declined again to 7.5 g. in the summer of 1947.

The results suggest that with constant application of fertilizers at least two to three years are necessary to achieve maximum production from the bottom fauna. Further, even after two and a half years had elapsed since regular fertilization was practised, the bottom fauna production was still more than twice as great as under 'natural' conditions.

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NOTES ON THE GENERAL BIOLOGY OF *TUBULARIA LARYNX* ELLIS & SOLANDER

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(Text-figs. 1-6)

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INTRODUCTION

Though *Tubularia* has been extensively used as material for experimental studies of regeneration (Barth, 1940), and though detailed accounts are available of the cleavage of the ovum and of the early stages of development of the actinula larva (Allman, 1871; Ciamician, 1879; Conn, 1882; Brauer, 1891; Lowe, 1926), little attention has been given to the general biology of this gymnoblast, though Allman (1871), Ciamician (1879) and Salensky (1911) have given some details of post-liberation changes in the actinula and Klugh (1929) has briefly described certain factors which affect the vitality of the fully developed colony. Studies of the settlement of marine organisms on toxic surfaces have shown that *Tubularia* is one of the organisms most resistant to such poisons as copper (Barnes, 1948), and this fact has led to investigations of various aspects of the general biology of this genus. The preliminary results of these investigations are presented in this paper.

The material upon which this study has been based can most satisfactorily be included in the species *Tubularia larynx* Ellis & Solander, though the

colonies which settle and develop upon suitable exposed surfaces at Millport differ in certain respects from the characters of this species as listed by Allman (1872). He gives the average height of a colony of this species as $1\frac{1}{2}$ –2 in. and states that the stems bear 'more or less distinctly marked annulations at intervals'. Colonies of this species at Millport generally exceed 3 in. and may reach 4 in. in height, and annulations are very difficult to detect on the stems; they are rarely clearly visible on the stems of a living colony, but a few shallow annulations can be seen on the bare stems after the polyps have been shed and the colony has died down to the condition in which it lives through the winter. It is felt, however, that differences of this character do not warrant the formation of a separate species for this material, though it is perhaps important that their existence should be mentioned. One further difference may be added. Mr J. Corlett (personal communication) has recently found, in the course of studies on the settlement of marine organisms in the Mersey, that there *T. larynx* does not flourish unless the water temperature exceeds 60° F. As at Millport this temperature is attained, under favourable conditions, only for a few days in the year, the temperature requirements of *T. larynx* at Millport appear to differ from those elsewhere, since there is no doubt that this species is able to settle in abundance and grow rapidly when the water temperature is well below 60° F.

Elmhirst (1923) states that the breeding period of *T. larynx* at Millport extends from May to September; our observations, made in greater detail over the past 5 years, are in general agreement with this estimate. Settlement is rarely at all heavy, however, until late in July. This period of heavy settlement continues through August and September and may extend into the first weeks of October. Some settlement may occur until the end of December.

During August and September, any suitable surface soon acquires a number of young colonies which grow rapidly. All the experimental material used in the present survey was taken from surfaces immersed from rafts moored close inshore. Sometimes colonies were removed from their substratum and brought into the laboratory for experiment. At other times, when it seemed essential to disturb the material as little as possible, colonies were used which had grown from settlements on ground-glass microscope slides immersed in the sea.

The use of settlement surfaces immersed from a raft is in some ways advantageous, in others the reverse. It is possible, using this method, to provide a surface, uncolonized by other organisms, for the attachment of the settling larva. Thus it is possible to obtain large numbers of settled individuals but, because of the conditions of immersion of these surfaces hung from a raft, the environment is not wholly normal. Continuous immersion is assured, but the immersed specimens remain at a constant depth below the surface of the water and consequently may be exposed to high light intensities for longer periods than are individuals growing normally just below low-water mark on a fixed object.

LIBERATION OF THE ACTINULA LARVA

As Lowe (1926) has shown, the developing actinula is orientated with its aboral pole pointing towards the opening of the gonophore and its oral pole, sheathed in the aboral tentacles, pointing inwards. Allman (1872, p. 407) has stated that in *T. larynx* the oral tentacles are not formed until after liberation, but it is clear from our material and from *T. larynx* from Plymouth that this statement is erroneous. The aboral pole thus emerges first as the actinula is expelled and the tips of the aboral tentacles last; as each aboral tentacle is freed, it stands out from the body of the larva, so that the newly liberated actinula has a number of aboral tentacles radiating stiffly outwards (Fig. 1A). Allman (1872) for *T. indivisa* L. and Ciamician (1879) for *T. mesembryanthemum* Allman, state that in these species the oral pole of the larva emerges first.

The factors affecting the liberation of the actinula larva are still largely unknown, but two possibilities have been investigated in the course of this work. Early laboratory experiments suggested that change in light intensity stimulated the liberation of actinulae, since the rate of liberation was increased immediately after transfer from light to darkness or from darkness to light. Later work, however, has not wholly substantiated this result, the average rate of liberation (i.e. the number of larvae liberated per hour) is greater in darkness than in light, but a change of light intensity does not invariably increase the rate of liberation of actinulae. This point requires fuller investigation under carefully controlled conditions.

The other factor investigated which affects the rate of liberation of actinulae was variation in current speed. The range of current speed that could be used was limited, and was generally low in comparison with that to which colonies are exposed during the ebb tide at Millport, but the results obtained strongly suggest that larval liberation is markedly reduced in quite moderate currents. At a water speed of 1 cm./sec. the rate of liberation was greater than that which occurred in still water, but if the speed of the current was increased to 3 cm./sec. liberation of actinulae practically stopped. These preliminary results suggest that liberation may only take place in the sea over slack-water periods. This point is of some importance in the distribution of larval settlement round a mature colony and will be discussed more fully later (p. 35).

Large numbers of actinula larvae can readily be obtained for experimental purposes by suspending mature colonies, polyps downwards, in fresh sea water. If the sea water is frequently renewed, liberation of actinulae will continue for several days. Thus, a group of colonies containing approximately 150 polyp heads liberated about 1000 larvae over a period of 6 days in the laboratory, an average of about seven larvae per polyp. This is almost certainly an underestimate, as it is reasonable to assume that some larvae had been shed before the colonies were collected and that the full development of others was

doubtless affected by the artificial conditions of the laboratory. Further, this estimate assumes that all the polyps in the colony liberated actinulae during the period of observation; as will be shown later, this is not likely to be true, so that it can be safely assumed that one polyp produces many more than seven larvae.

THE ACTINULA LARVA

Morphological changes before settlement

Immediately after liberation from the gonophore, the actinula larva of *T. larynx* consists of an ovoid body with the mouth, surrounded by four or five short oral tentacles, at one pole, and some distance below it a number of long aboral

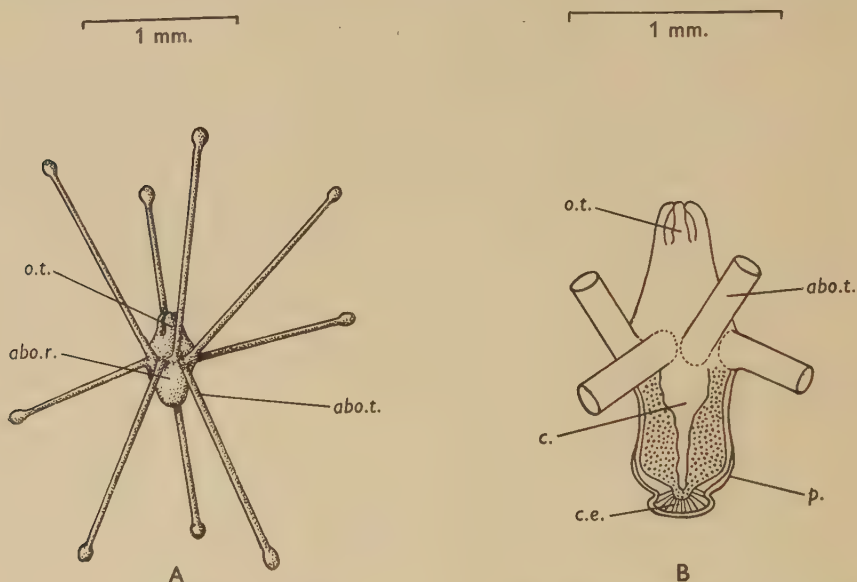


Fig. 1. A, actinula larva of *Tubularia larynx*, immediately after liberation. B, semi-diagrammatic sketch of the body of the actinula larva of *T. larynx*, shortly before settlement. The aboral region is shown in optical section. *abo.r.*, aboral region; *abo.t.*, aboral tentacle; *c.*, coelenteron; *c.e.*, columnar ectoderm; *p.*, perisarc; *o.t.*, oral tentacle.

tentacles which radiate stiffly outwards (Fig. 1A). The tips of these tentacles are swollen and within the superficial tissues of these swellings are large numbers of nematocysts. The number of these aboral tentacles varies. In a series of some 200 actinulae, the number of aboral tentacles varied from six to thirteen, most (32 %) had ten aboral tentacles and over 75 % had nine, ten or eleven aboral tentacles.

Shortly after liberation, that part of the body below the aboral tentacular ring (the aboral region) begins to elongate. Immediately after liberation this aboral

region measures 0.3 mm. in length and is 0.32 mm. in diameter at its widest part. When settlement occurs, this part of the larval body has increased in length to 0.43 mm. and its diameter has decreased slightly, now being 0.28 mm.; it is thus distinctly cylindrical in form (Fig. 1B).

The surface of the aboral pole of the actinula can be seen to be covered by a thin membrane immediately after liberation. By the time this region of the body has elongated, this membrane, which is the first appearance of the perisarc, can readily be distinguished (Fig. 1B). Some of the properties of this sheath were investigated using larvae which had settled on the substratum, since the sheath is then attached and can be manipulated more easily. If such larvae are placed in 10 % NaOH, rapid and extensive maceration of the tissues takes place and the body of the larva can be drawn out of the sheath, leaving the latter as a short cylinder, closed at one end, attached to the substratum. The sheaths may then be washed several times and can be stored either in tap water or in 4 % sea-water formalin.

When treated with Mallory's triple stain, the sheath stains a deep blue; it dissolves slowly in cold concentrated HCl; it is not wholly soluble in 50 % NaOH at 60° C., and it gives a faint positive reaction to the chitosan test (the difficulty in obtaining a more satisfactory result to this test lies in the manipulation of the material). These properties are such as strongly to suggest that this sheath is chitinous in nature. One further point of interest emerges from these experiments; when treated with warm, concentrated alkali, the sheaths do not dissolve (though they become appreciably more delicate), but they always become detached from the substratum, suggesting that they are attached by a substance soluble in concentrated alkali. It is, therefore, possible that attachment is secured by means of an extra-chitinous cement similar to that found in arthropods. Mr B. W. Sparrow (personal communication) has demonstrated the existence of dihydroxyphenols in the attachment cement of *T. larynx*, an observation which strongly supports this possibility. There are indications (see also p. 29) that the cement used for the attachment of a number of marine animals belonging to different phyla may consist of a mucoprotein, and that this mass of cement hardens in a manner similar to that described for the arthropod cuticle by Pryor (1940). Ciamician (1879) suggested that the chitinous perisarc itself served to attach the actinula larva of *T. mesembryanthemum* to the substratum, but this seems unlikely to be true for the recently settled actinula of *T. larynx*.

General biology of the larva

After liberation, the actinula larvae sink slowly through the water. Measurements indicate that they sink at a rate of about 1 mm./sec., so that, although they may be carried in a slight current a little distance from the parent colony, it is probable that many will come into contact with a substratum not far from their point of liberation.

The aboral tentacles of the unattached actinula are held alternately pointing away from the substratum and towards it (Fig. 1A) and the larva can move slowly on the tips of the latter set of tentacles. Progress in this way is slow, but appears faster in light (of the order of 0.3 cm./hr.) than in darkness (roughly 0.1 cm./hr.). Critical experiments have not yet been made, but an examination of the results of these preliminary experiments suggests that the larvae are photokinetic rather than phototactic.

During this period of free movement over the substratum the orientation of the larva is mainly that which is eventually assumed, namely with the aboral pole towards the substratum. This point was specially examined as other accounts of the orientation of actinula larvae (e.g. Allman, 1872, for *T. indivisa*) suggest that the oral pole is directed towards the substratum and that a reversal of this orientation takes place just before settlement.

Temporary attachment to the substratum can take place by means of the tips of the aboral tentacles, but it would seem that these tentacles do not become attached immediately the larva comes into contact with a substratum. An actinula larva, placed in a dish of sea water and allowed to sink to the bottom, can at first be moved by the slightest current, but if larvae are left in contact with the substratum for a period of 2 hr., and are then subjected to a current which is very gradually increased in speed, they can withstand much faster currents. Most of the larvae became dislodged when the current speed was increased to 1–2 cm./sec., but some could withstand currents up to 8 cm./sec. before being dislodged. These results were obtained using smooth glass surfaces; under natural conditions, where the substratum may be more suitable for attachment and where the rate of increase of current speed is probably less, it may be that much stronger currents can be withstood without the larva becoming dislodged. It was frequently noted that when a larva became dislodged in a weak current it did not move far, but became attached again within a short distance (e.g. 3 cm.) of its original point of attachment. Much stronger currents were then needed finally to dislodge such larvae.

In the laboratory a considerable time interval may elapse before an appreciable proportion of actinulae become attached permanently to the substratum. Table I gives typical examples of the progress of attachment.

TABLE I. SETTLEMENT OF ACTINULAE OF *TUBULARIA LARYNX*

First-crop larvae		Second-crop larvae	
Estimated time after liberation (hr.)	Percentage attached	Estimated time after liberation (hr.)	Percentage attached
14	5	6	44
18	12	11	84
22	39	16	96
28	71	25	100
37	96		
46	100		

To obtain actinula larvae for these experiments, mature colonies of *T. larynx* were collected during the morning and inverted in fresh sea water for approximately 6 hr. The actinulae shed during this period were then collected and form the 'first-crop larvae' of Table I. The sea water bathing the colonies was then changed and the colonies were allowed to stand overnight. Actinulae were again collected the next morning and form the 'second-crop larvae'. There is clearly a very considerable difference in the rate at which these two batches of larvae become attached; this point is discussed more fully in the next section. It is evident, however, that the period for which the larvae are unattached may be greater than that recorded by Ciamician (1879) for the actinulae of *T. mesembryanthemum* (4-6 hr.). It will be noted that all the larvae eventually succeeded in becoming attached. Such results were typical of these larvae; under normal environmental conditions the proportion which settled successfully was rarely less than 90%. Other factors affecting settlement are discussed in the next section.

SETTLEMENT

It is not possible to give an account of the actual process of settlement, since this stage in the life history is apparently accomplished without the appearance of any marked structural changes or the initiation of any characteristic reactions. Sometimes the aboral tentacles lose their rigidity at about the time that settlement occurs; but this does not always seem to be so, and it is possible that this change is due to the artificiality of laboratory conditions. Larvae have frequently been watched carefully over the whole period between liberation and settlement, and it has not been possible to observe any marked or invariable change in structure or habit which would indicate that a larva was about to settle.

The effect of a number of factors on settlement has been investigated. The results obtained are briefly summarized below.

(i) *Hypotonic Sea Water.* Actinula larvae of *T. larynx* are not capable of withstanding hypotonic conditions for prolonged periods but, although degenerative changes were evident in the mixtures containing smaller proportions of sea water, there was also a tendency for settlement to be accelerated in such solutions (Table II).

TABLE II. SETTLEMENT IN FULL AND DILUTED SEA WATER

Estimated time after liberation (hr.)	Percentage attached		
	Sea water	70 % sea water	60 % sea water
7	0	24	20
9	3	42	20
20	7	43	36

(ii) *Copper and Mercury.* Grave & Nicoll (1939) have recorded that copper stimulated the attachment of ascidian larvae, and Prytherch (1934) considered that increased amounts of copper present at low water caused the settlement

of the larvae of *Ostrea virginica* in Milford Harbour, though his conclusions have been severely criticized by Korrington (1940). A number of rough experiments on the effect of the addition of small amounts of copper and of mercury to sea water on the attachment of actinula larvae were carried out and the results suggest (Table III) that both of these poisons stimulate attachment to some extent.

TABLE III. EFFECT OF COPPER AND MERCURY ON SETTLEMENT

Estimated time after liberation (hr.)	(1) Copper				
	Percentage attached				
	Sea water	0.05 mg./l. Cu	0.075 mg./l. Cu	0.1 mg./l. Cu	0.25 mg./l. Cu
6	0	0	3	14	78.1
9	3	0	6	16	80
19	7	0	39	46	100
28	24	35	50	60	100

Estimated time after liberation (hr.)	(2) Mercury				
	Percentage attached				
	Sea water	0.01 mg./l. Hg	0.05 mg./l. Hg	0.1 mg./l. Hg	0.25 mg./l. Hg
10	0	36	40	82	100
27	80	53	66	90	100

The range of copper and of mercury concentrations used in these experiments includes concentrations that are toxic. The median lethal concentration of copper (for an exposure period comparable with the total length of the experiment recorded in Table III) is approximately 0.09 mg.Cu/l., whereas the corresponding figure for mercury is 0.03 mg.Hg/l. Attachment is, therefore, stimulated at concentrations below the median lethal concentration for both poisons and, though the larvae in the highest concentrations were dead at the end of the experiment, attachment had taken place before death occurred.

(iii) *Benzoquinone and Ascorbic Acid*. If small amounts of these compounds are added to sea water in which actinula larvae have been placed, there is, up to concentrations which are toxic, a stimulatory effect on attachment. Table IV shows the results of one experiment using benzoquinone.

TABLE IV. EFFECT OF BENZOQUINONE ON SETTLEMENT

Estimated time after liberation (hr.)	Percentage attached				
	Sea water	0.01 mg./l. BQ	0.1 mg./l. BQ	1.0 mg./l. BQ	10.0 mg./l. BQ
15	23	36	37	0	0
27	40	74	91	0	0

At concentrations higher than 0.1 mg. benzoquinone/l. this compound killed the larvae very shortly after immersion in the solution.

Comparable results were obtained using ascorbic acid.

A brief explanation should perhaps be given of the reasons why the effect of these two rather unusual reagents was tested. Observations by one of us (K. A. P.), referred to in Harris (1946), suggest that the cement which is used to attach a number of sedentary marine animals (barnacles, mussels) to the substratum is formed from a mucoprotein basis, which is 'tanned' by the action of a quinone, in a manner similar to that described by Pryor (1940) for the cuticle of insects. It seemed possible that the cement which attaches the stolonial perisarc of *Tubularia* to the substratum was of a similar nature and the effect of these compounds was therefore investigated to test this possibility. Benzoquinone was used to provide a quinone already present in solution (in the insect cuticle the quinone is formed by oxidation from the corresponding dihydroxyphenol) and so possibly to 'tan' the mucoprotein rapidly and so prevent attachment because the mucoprotein cement had not spread sufficiently. The effect of ascorbic acid was investigated because this compound has been found (Evans & Raper, 1937) to be capable of reducing dopa quinone to dopa in the tyrosinase—tyrosine reaction (which in some respects parallels the reactions which occur as a mucoprotein becomes 'tanned'). The effect of the addition of ascorbic acid might, therefore, be to prevent 'tanning' of the mucoprotein of the cement by the prevention of oxidation of the dihydroxyphenol to the corresponding quinone. Apart from the stimulatory effects noted in Table IV, no particular effect on attachment was produced by either of these reagents.

(iv) *The presence of bacterial slime.* All the experiments on the rate of settlement of the actinula larva so far described were carried out in clean glass vessels. Such a substratum is probably highly abnormal, and an attempt was made to produce a substratum which was slightly more normal by carrying out settlement experiments in glass dishes in which sea water had been allowed to stand for a week. When this was poured away, a thin slime film, probably bacterial in origin, was present over the bottom and sides of the dish. Settlement was appreciably heavier on this surface than on a clean glass surface 24 hr. after the addition of freshly liberated actinula larvae.

The general impression gained from this series of experiments is that a variety of conditions can stimulate attachment. In fact, the reaction of an actinula larva to a disadvantageous environment seems to be that it becomes permanently attached. The reason for this may well be in the sequence of changes that takes place between liberation and settlement. The ectoderm at the tip of the aboral pole of the actinula larva is deeply columnar and its cells are packed with dark granules. The general appearance of this tissue, which is clearly discernible before the larva is liberated (Lowe, 1926), suggests that it is secretory in function. It would seem likely that this region of the ectoderm secretes the attachment cement, and it begins to do so when the aboral pole of the larval body comes into contact with the substratum. Normally this cannot happen until this region of the body has elongated, since the stiff aboral tentacles hold it away from the substratum. If, however, the aboral tentacles were to lose their rigidity for any reason, this 'fixation area' would prematurely be brought into contact with the substratum. As one of the first effects of a disadvantageous environment is to cause the aboral tentacles to lose their rigidity, it seems plausible to suggest that this is the reason why such a diverse series of conditions produce a similar effect.

The suggestion advanced in the preceding paragraph involves the assumption that the secretion of cement is possible whenever the aboral pole of the larva comes into contact with the substratum. Direct experimental proof that this assumption is correct is not yet available, but a number of observations, both under laboratory and under field conditions, suggest that this is so. Under laboratory conditions the high percentage settlement almost invariably obtained suggests that attachment is a passive process in the sense that it occurs as soon as the requisite part of the body comes into contact with a substratum, and, under field conditions, the wide range of substrata upon which settlement can occur also supports this suggestion. Settlement will not only take place readily on smooth surfaces such as glass or bakelite, and not only on rather rougher and more irregular surfaces such as ground glass or the compartments and opercula of barnacles, but also on substrata which are unstable and upon which practically no other sedentary animal seems able to settle. For example, the surface of certain types of resin-containing compositions soon becomes coated with a thick layer of jelly-like slime, which is probably bacterial in origin and which forms a most unstable substratum; actinula larvae settle in numbers on such slimes, though the young colonies are lost as soon as the slime layer peels away from the paint surface beneath. Again, anti-fouling compositions containing cuprous oxide which have a leaching rate which lies between 10 and 20 mg. copper/m.²/day, acquire a felt-like algal settlement (formed, at least in part, by *Ectocarpus*) which soon completely covers the paint surface: *Tubularia larynx* is one of the few organisms which can settle and grow on this type of surface.

Algal growth of other kinds, such as *Enteromorpha* or the more normal tufted growth form of *Ectocarpus*, generally prevents settlement, but this effect is only evident if the algae exceed a certain length. In the course of exposures made to study the settlement and growth of *Tubularia larynx*, which are described more fully in the next section, it was found that settlement of the actinulae occurred readily in the presence of these algae if the latter did not exceed 2 mm. in length. This suggests that sporelings of greater length, provided their settlement was sufficiently dense, were perhaps capable of preventing contact between the actinula and the substratum. Occasionally actinula larvae succeed in settling on the filaments of well-grown *Ectocarpus*, and settlement will occur readily on the fronds of *Laminaria*, observations which suggest there is little inimical in an algal surface *per se*.

POST-SETTLEMENT CHANGES

Growth and maturity

The changes which take place in the actinula larva immediately after settlement are shown in Fig. 2. Fig. 2A shows a young form very shortly after settlement has taken place; Fig. 2B the same individual just over 7 hr. later, and Fig. 2C

its appearance after a lapse of a further 12 hr. These figures emphasize the extremely rapid elongation which occurs immediately after settlement; over a period of some 19 hr. the overall length increased from 0.98 to 1.65 mm. The cell layers of the body wall become much thinner during this process and it would, therefore, seem that this elongation is due rather to the redistribution of tissue already formed than to the production of new tissue.

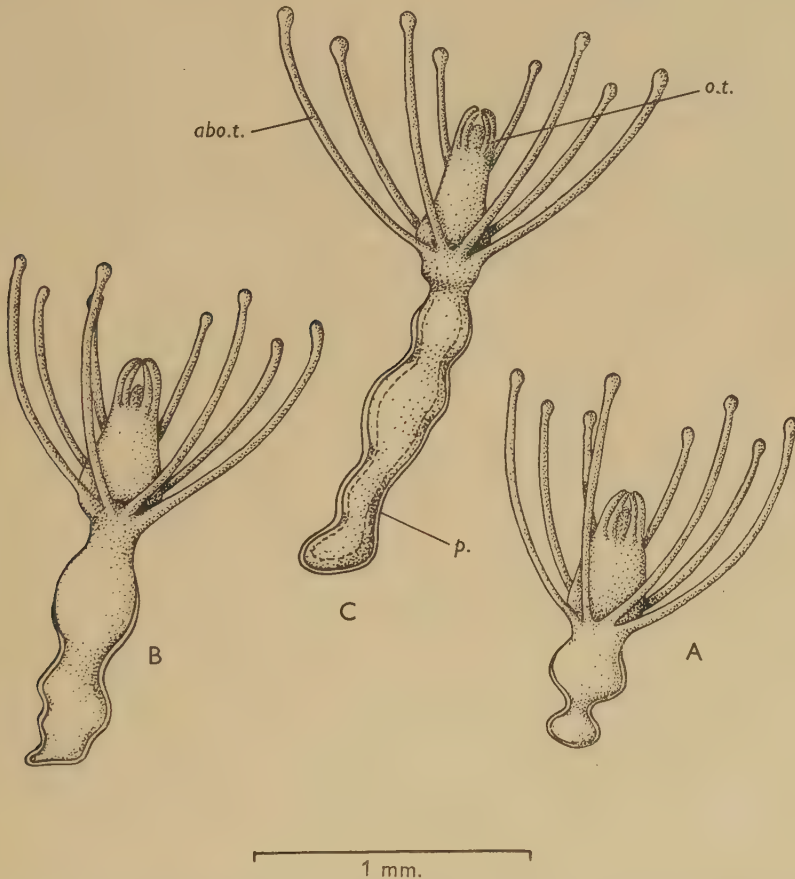


Fig. 2. Newly settled individuals of *Tubularia larynx*. A, shortly after settlement. B, approximately 7 hr. after settlement. C, approximately 19 hr. after settlement; the broken line within the aboral region indicates the inner boundary of the endoderm. *abo.t.*, aboral tentacle; *p.*, peristome; *o.t.*, oral tentacle.

The lower part of the stem of the young individual and the short length of primary stolon are both formed from the aboral region of the actinula larva. It is difficult to decide what relation these two derivatives bear to the original point of attachment, but it seems plausible to suggest that elongation on one side of this point leads to the production of stolon, whereas elongation on the

other side leads to the production of stem. For the latter, it must be presumed that elongation is initially not equal at all points, since the stem bends sharply away from the substratum. The aboral tentacles, it will be noted, are now all directed away from the substratum, but their tips are still swollen at this stage; they lose this characteristic later.

Following this stage of elongation there is one in which growth of the stolon predominates. This part of the colony may measure 0.3 mm. in length shortly after settlement has been achieved; 2 days later its length is 0.8 mm., and after a further 2 days 1.3 mm. At this stage a second polyp often appears, usually arising from the tip of one of the branches of the stolon and growing rapidly upwards. Growth of the stolon continues to predominate for some time longer, so that 11 days after settlement a total length of stolon of 7 mm. may be present (made up of a number of branches) associated with about eight polyps. Once a branching stolonial system has been established in this way, it is probable that further growth of the colony chiefly results in the production of stems and polyps.

Gonophore buds appear very early. For example, buds were visible between the oral and aboral tentacles on the primary polyp by the time the second polyp appeared and they are generally present some 7 days after settlement. The gonophores grow rapidly and just over 3 weeks (24 days) after settlement a number are capable of shedding actinulae. This estimate of the period taken to reach maturity is considerably longer than that found by Orton (1929) at Cawsand Bay, Plymouth, though comparable with the estimate he gave in an earlier paper (Orton, 1914). The diameter of the polyps is then 2 mm. measured across the base of the aboral tentacles. Growth of the polyps continues for a further fortnight during which large numbers of actinulae are shed, after which autotomy of practically all the polyps occurs. It is of interest to note that, when the colony is fully developed, only a proportion of the polyps are capable of liberating actinulae, yet when autotomy occurs, practically all the polyps are lost. This indicates a certain degree of differentiation of function among the polyps of a well-developed colony, in that while all can presumably feed, only a limited number produce larvae. The polyps lost are later replaced by others, which develop from the tips of the stems of the established colony. Presumably this second set of polyps may themselves grow, develop gonophores, shed actinulae and finally be lost, but it has not yet been possible to carry out field observations for long enough to prove this point. Successive 'generations' of polyps certainly appear under laboratory conditions, though their gonophores may not reach full development.

Factors affecting the growth and development of the colony

Observations have been made on the general biology of colonies of *Tubularia larynx* by exposing standard microscope slides (3×1 in.), with one face slightly roughened (using 80-mesh carborundum powder), on painted steel plates

adapted to act as carriers for these slides. Each side of each plate can accommodate 27 slides, arranged in three rows, 9 slides to a row. These steel carriers can readily be bolted to the standard frames used for the exposure of painted steel plates; extensions to the frames allow carriers to be immersed at a number of depths. Exposures of this kind were made in 1946 and 1947, four carriers being used on each occasion; they were immersed at depths of 27, 45, 64 and 84 in. (approximately 0.7, 1.1, 1.6 and 2.1 m.) below the water surface. One slide was withdrawn from each row of each face of each carrier at approximately weekly intervals (the period between withdrawals was varied slightly according to the amount of change that was taking place at the time) and replaced by a clean slide. These slides which were withdrawn at intervals over the whole period of the experiment are termed the basic series in the description below. The slides which replaced them were themselves later withdrawn, some at approximately weekly and some at approximately 3-weekly intervals—these slides formed the weekly and the 3-weekly series mentioned later. After withdrawal, each slide was examined in detail and its various settlements and their characteristics recorded.

The slide series were immersed on 31 July both in 1946 and 1947. In 1947 immersion was continued until 10 October, but in 1946 the exposure period only lasted until 19 September.

Fig. 3 gives the general results of growth-rate measurements in 1946 and 1947. It was clearly impossible to attempt to measure growth by measurements of individual colonies, as only a few colonies could be dealt with in this way at the expense of a great amount of labour. As a rough estimate, therefore, the volume of *Tubularia* on each slide was determined. Using this method the growth on a number of slides could be rapidly estimated; the disadvantage was that reliable measurements were not possible until some time after settlement, as volumes less than 0.2 ml. could not be measured with sufficient accuracy. The results shown in Fig. 3 indicate that the initial growth rates were substantially the same in both years.

When, however, the numbers of new settlements per slide on the basic series of slides are compared for the 2 years (Fig. 4), considerable differences are evident. In 1946 the numbers of new settlements recorded showed a sharp increase between 4 and 5 weeks after the experiment began, whereas in 1947 the increase was much smaller, though it occurred at approximately the same time after immersion. Evidence will be presented later which suggests that the number of new settlements depends upon the state of maturity of the polyps in the immediate vicinity, i.e. those on the same slide or on its neighbours. The results obtained in 1946, therefore, indicate that considerable numbers of actinulae were released at almost the same time; but those obtained in 1947 may mean either that the numbers were much smaller (owing to poor development of the polyps) or simply that the actinulae were not able to settle.

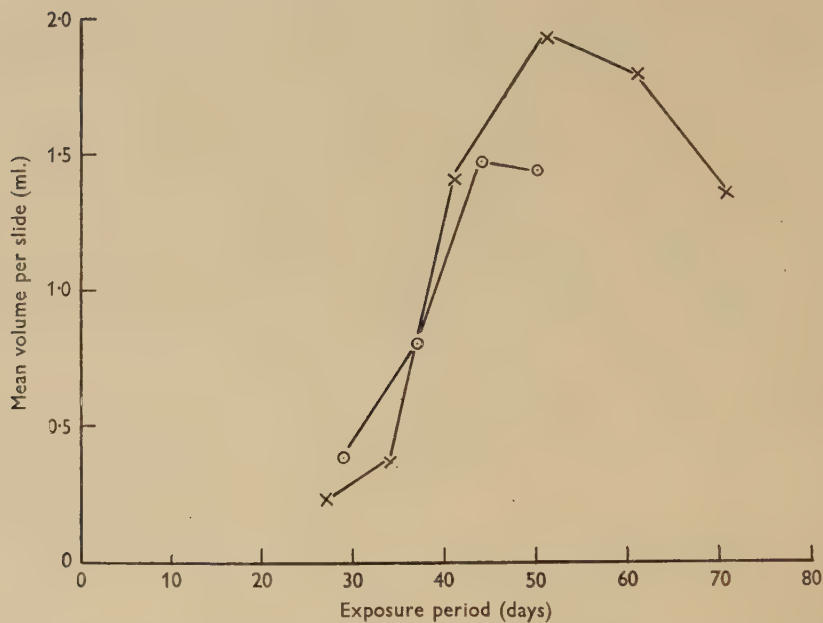


Fig. 3. Growth rates of *Tubularia larynx* in 1946 and 1947 (as indicated by increase of volume of the colonies) on the basic series of slides. —○—, 1946; —×—, 1947.

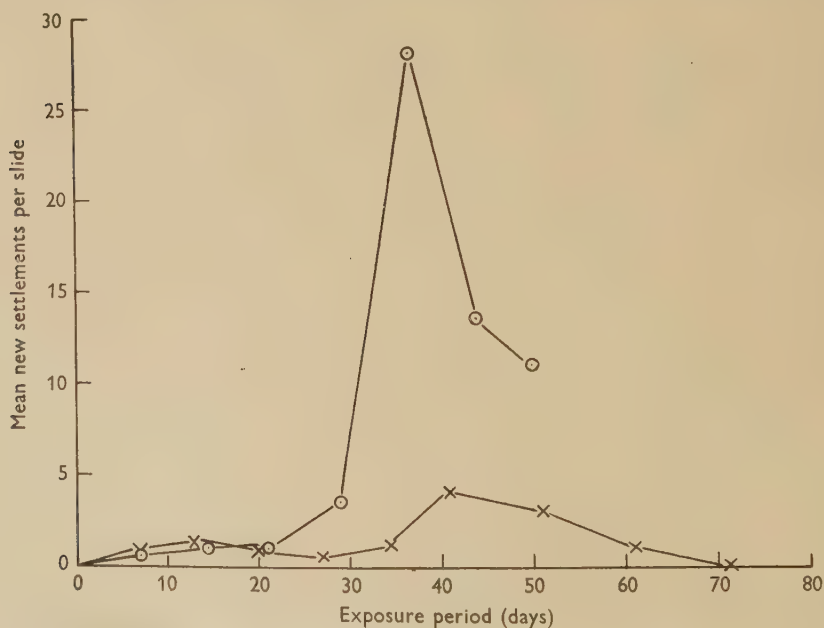


Fig. 4. New settlements of *Tubularia larynx* in 1946 and 1947, on the basic series of slides. —○—, 1946; —×—, 1947.

Other evidence suggests that the second explanation is probably correct. The first 5 weeks of the exposure period in 1947 were characterized by an unusually high proportion of sunny, calm days and the light intensity down to the depth covered by these slide exposures was probably greater than that for the corresponding period in 1946. This difference in environmental conditions would favour the growth of algae and, as is shown in Table V, their settlement was certainly heavier at all depths, and growth, at least of *Ectocarpus*, greater at all depths in 1947 than in 1946.

TABLE V. SETTLEMENT AND GROWTH OF ALGAE AT VARIOUS DEPTHS,
AUGUST 1946 AND AUGUST 1947

Depth below sea level		<i>Enteromorpha</i> sp.		<i>Ectocarpus</i> sp.	
In.	M.	1946	1947	1946	1947
27	0·7	V. Fr. (4·8)	V. Fr. (2·5)	V. Fr. (6·6)	V. Fr. (7·6)
45	1·1	Occ. (s)	Fr. (s)	Occ. (s)	Fr. (5·6)
64	1·6	Rare (s)	Fr. (s)	Rare (s)	Fr. (3·8)
84	2·1	V. Ra. (s)	Fr. (s)	V. Ra. (s)	Rare (1·0)

V. Fr., Very Frequent; Fr., Frequent; Occ., Occasional; V. Ra., Very Rare.

The figures in parentheses are the mean lengths (in mm.) of the algal filaments. (s) indicates present only as sporelings.

These results refer to the basic series of slides; the 3-weekly and the weekly series, since their exposure periods are shorter and their chances of extensive algal colonization therefore less, should, if this suggestion is correct, indicate numbers of settlements which are more comparable for the 2 years. The results shown in Fig. 5 are in agreement with this suggestion. As might be expected, the difference between the 3-weekly series of 1946 and that of 1947 is greater than that between the weekly series; the numbers of new settlements on the latter are, within the limits of accuracy of an experiment of this sort, closely similar in 1946 and 1947.

Counts of the number of new settlements on slides exposed at various depths in 1946 showed that settlement did not take place predominantly at any of the depths investigated, but measurements of the mean volume of colony per slide at different depths suggested that the colonies attained a greater size when growing at depths greater than 4 ft. (1·2 m.) than they did when growing nearer the surface.

The presence of a mature colony contributes substantially to the amount of settlement which takes place in its immediate vicinity. When the experiments described earlier in this section were started, surfaces only a few feet away from the slide carriers bore large numbers of mature colonies of *Tubularia larynx*, yet settlement on the slides did not become heavy until some weeks later. This result might have been due to one of two causes; either the surfaces were, for some reason, not suitable for settlement immediately after immersion, or heavy settlement must be dependent upon the close proximity of mature colonies.

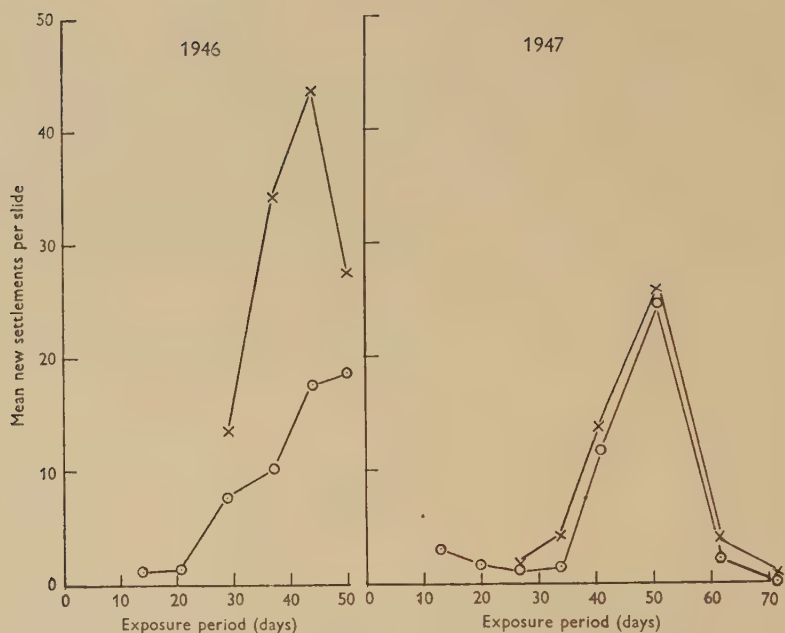


Fig. 5. New settlements of *Tubularia larynx* in 1946 and 1947, on the weekly and 3-weekly series of slides. —○—, weekly series; —×—, 3-weekly series.

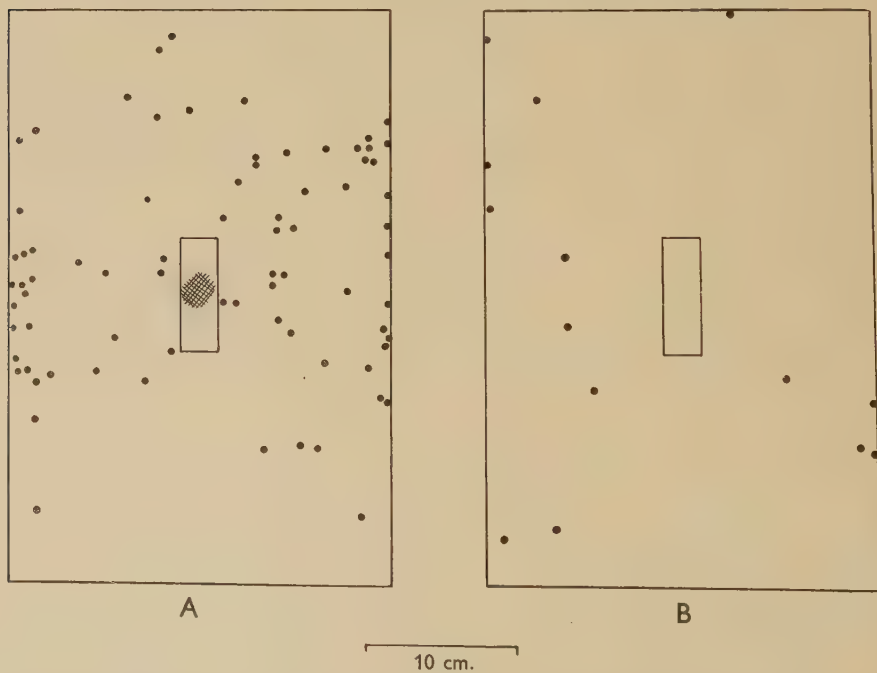


Fig. 6. New settlements of *Tubularia larynx* on (A) a wooden panel with a glass microscope slide fixed centrally bearing a colony of *T. larynx* and on (B) the same with the microscope slide clean. The position of each new settlement is indicated by a black circle.

Moore (1939) has described the lag in colonization of a newly prepared artificial surface, and it seemed conceivable that newly immersed glass slides might show a comparable lag. That this was not the factor which delayed settlement of the actinulae of *T. larynx* was clearly shown by an experiment in which freshly prepared slides were immersed beside slides which had been in the sea for some weeks, but which had their gross fouling removed. Settlement and growth on the two series was found to be closely similar.

This result suggests that the second possibility is the more likely and this is supported by the following experiment. A glass slide, bearing a mature colony of *T. larynx*, was set in the middle of a wooden panel, 10 × 15 in., and immersed from a raft which itself bore practically no *Tubularia*; a control exposure consisting of an uncolonized slide set in the middle of a similar panel was immersed close beside it at the same time. The amount of settlement on the two surfaces after a period of 11 days' immersion is shown in Fig. 6, and clearly indicates the heavier settlement which occurs in the vicinity of a mature colony.

BIOTIC ENVIRONMENT

Once settlement has been achieved and growth begun other organisms soon begin to be associated with, or to prey upon, the colony of *Tubularia larynx*. Under the conditions in which most of the colonies were studied in this investigation, where the colony of *T. larynx* was the largest colonizing form, the bases of the colonies soon began to accumulate the muddy tubes of *Jassa* sp., and also frequently bore clusters of small mussels (*Mytilus edulis* L.) which are usually settling in some abundance at the time that settlement of *Tubularia larynx* is becoming intense. The stems of the colonies quickly became colonized by Suctorians, chiefly *Ephelota* sp. and *Acineta* sp. The settlement of these Protozoa appeared to be successive in 1946, as *Ephelota* sp. predominated until early September, whereas *Acineta* sp. was more common later in the season. Diatoms, especially *Licmophora* spp. and *Striatella* sp., were also conspicuous on the stems of well-grown colonies, especially towards the end of September or early in October; the colonies of *Tubularia larynx* were then sometimes dark brown in colour due to the dense covering of these diatoms.

All these forms are merely associated with the colonies of *T. larynx*, and do not appear to have any predatory or parasitic relationships with the hydroid. Others, however, are predators or parasites.

The pycnogonid, *Phoxichilidium tubulariae* Lebour, is commonly to be found among colonies of *Tubularia larynx*, a habitat similar to that recorded by Lebour (1945) for *Phoxichilidium tubulariae* at Plymouth. The larvae of this pycnogonid occur within the gastral cavity of *Tubularia larynx* and, though a few larvae can usually be detected in this situation late in September, they seem only to be really abundant if well-developed colonies of *Tubularia* are present in some abundance at this time. Normally *T. larynx* is beginning to die down at the

end of September, but if, as in 1945, it is flourishing early in October, practically every colony has several polyps which contain the larvae of *Phoxichilidium tubulariae*. Development of the latter must be rapid, as on one occasion colonies of *Tubularia larynx*, collected from a surface that had been immersed for only 24 days, contained advanced larvae of *Phoxichilidium tubulariae*. As some part of this immersion period must have been occupied by settlement and initial growth of the *Tubularia* colony, it is reasonable to suppose that the larvae of *Phoxichilidium* must have developed to this stage in less than 20 days. Lebour (1945) states that these larvae do not appear to harm the polyp in which they occur. We have found that such a polyp is usually abnormally distended, but that it seems otherwise normal. Because colonies of *Tubularia larynx* are so resistant to copper, experiments have been carried out in which this hydroid was immersed in copper solutions of different concentrations; on some occasions colonies with polyps containing the larvae of *Phoxichilidium tubulariae* were used for these experiments, but the sensitivity of infected colonies to this poison did not differ appreciably from that of colonies in which the polyps were uninfected.

The Holotricha, *Choenia* sp. and *Loxophyllum* sp., are also commonly found on colonies of *Tubularia larynx*. *Choenia* sp. is the more abundant: it feeds on newly settled forms, and is to be found in large numbers on mature polyps shortly before these are lost and also on and in moribund stems.

Numbers of nudibranch molluscs, particularly *Cratena aurantia* (Alder & Hancock) and *Dendronotus frondosus* (Ascanius), occur about the time that settlement and growth of *Tubularia larynx* reaches its maximum. Both feed on the polyps; the numbers of *Cratena aurantia* which occur suggest that this species may play a significant part in the reduction in the numbers of polyps which takes place at the end of the season. It would seem unlikely, however, that *C. aurantia* is the primary cause of this reduction.

DISCUSSION

General observations in the field, as well as the results of experimental work, indicate that settlement of actinula larvae is heaviest in the immediate vicinity of a mature colony, which suggests that settlement occurs shortly after liberation. Laboratory observations, on the other hand, indicate that a period of the order of 24 hr. must elapse before an appreciable proportion of the larvae become attached. This discrepancy may occur because of the unnatural conditions under which laboratory observations must be carried out, but as observations suggest that in a healthy actinula larva elongation of the aboral pole of the larva must occur before the attaching surface can come into contact with the substratum, it would be expected that an interval should elapse between liberation and attachment in the sea. In fact, it is conceivable that under field conditions the interval might be slightly longer, since the water temperature is lower in the sea than in the laboratory. It is not known how the larva

remains in contact with the substratum during this interval, but experiments carried out in the course of this investigation suggest that it is capable of remaining attached, even to a smooth, clean glass surface, in moderate water currents. In a more natural environment, attachment is likely to be more secure.

The actual means whereby this initial attachment is effected are not yet certainly known. It is possible that the tips of the aboral tentacles adhere to the substratum by means of an adhesive secretion (Orton (1929) speaks of the actinula larva of *Tubularia larynx* as 'highly adhesive'), but the experimental results do not agree well with such a hypothesis. For, if an adhesive secretion is produced, it is perhaps possible that the amount of this secretion might be increased under the stronger stimulus of faster water-flow, but it is more difficult to see why a decrease in the current, followed by a more sudden increase, should almost always cause the larvae to be dislodged. Another possibility is that attachment may be effected by means of nematocysts. The swollen tips of the aboral tentacles contain large numbers of nematocysts which, to judge by the extreme ease with which this part of these tentacles becomes attached to a needle, may be very sensitive to mechanical stimuli. Ewer (1947) has recently shown that the tentacles of the buds of *Hydra vulgaris attenuata* become attached temporarily to the substratum by means of atrichous isorhizas which lie in the nematocyst batteries in the tentacles; it would seem possible that at least some of the nematocysts in the tips of the aboral tentacles of the actinula larva have a similar function.

The results of the experiments on the effect of different current speeds on the rate of liberation of actinulae (though these experiments can only be regarded as preliminary in nature) are of interest, in that they suggest that larval liberation takes place only at periods of the tide when the larvae are least likely to be swept away in rapid tidal currents. They are in agreement with observations made on plankton hauls taken in the vicinity of mature *Tubularia* colonies. Tow-nettings have regularly been taken, during the ebb tide, from a point only a few yards from a raft bearing hundreds of mature colonies of *T. larynx*, but only individual larvae have been found when the haul was examined. Even if a plankton net is placed close against the side of a plate bearing large numbers of mature colonies, the result is much the same. This suggests that the number of larvae present in the water when the tide is running strongly is very small but, whilst this supports laboratory observations on the effect of current speed on the liberation of actinulae, these field results must be cautiously interpreted since many larvae may be caught up in the meshes of the net.

If further work substantiates the preliminary results of the effect of different current speeds on the rate of liberation of larvae, the question is then raised of the nature of the stimuli which initiate and stop liberation. Liberation of actinulae can be almost completely inhibited (in still water) by the addition

of small amounts (0.5 %) of NaCl, KCl and CaCl_2 ; the effect of potassium in this respect can partly be antagonized by the simultaneous addition of MgCl_2 . These results, which are closely parallel to the effects of these metallic ions on the contraction of smooth muscle, suggest that the immediate cause of liberation is contraction of the muscular elements of the gonophore, but do not indicate the nature of the stimulus responsible for initiation of the contraction. Further work is needed on this point.

A number of the observations made in the course of this work suggest that the colony of *T. larynx* should be regarded as a unit to a degree greater than that which is sometimes accorded to a hydroid colony. Some degree of functional differentiation among the individual polyps (in that only a small proportion bear mature reproductive organs) and the possibility that the life period of a single polyp is shorter than that of the colony both suggest that the unit is the colony rather than the polyp, and that the activities and development of the latter depend upon the general state of the former. When the colonies die down at the end of September or at the beginning of October, it is not easy to discover any external cause of this change. No rapid changes are taking place in water temperature and, though the depredations of *Cratena aurantia* (A. & H.) and other nudibranchs cause the loss of some polyps, such effects are commonly no greater than they have been for some time earlier. Further, the fact that, at the time when the main mass of *Tubularia* colonies which have provided the bulk of the season's growth are dying down, a small number of new settlements are growing makes it unlikely that any external factor is the cause of the general decline. Hammett (1946) concludes that endogenous factors play an important part in the general economy of *Obelia* colonies towards the end of their period of abundance, and it is difficult to resist the conclusion that such factors also play an important part in causing the degeneration of colonies of *Tubularia larynx* at the end of the summer.

Settlement and growth of *T. larynx* at Millport normally reach their maximum during August and September, but the general seasonal sequence is not always regular. In 1945 heavy settlement began early rather than late in July, but at the beginning of August all the colonies became moribund, and autotomy of the polyps occurred. Regeneration did not take place until the middle of September and then the main mass of the *Tubularia* settlement persisted until towards the end of October. There were some signs that a similar phenomenon was about to take place early in August 1947, but the process of decline was arrested at an earlier stage and the period of vigorous growth and development was not substantially interrupted. The causes of such variations in the normal seasonal sequence are unknown, since no disadvantageous environmental factor, either edaphic or biotic, could be detected over the period when the interruption occurred. The observation that vigorous growth can persist through October, if the normal seasonal sequence has been

interrupted by a period when the colonies are dormant does, however, offer some support for the suggestion that endogenous factors play a part in the autumnal decline of this hydroid.

We are indebted to the Marine Corrosion Sub-Committee of the British Iron and Steel Research Association for permission to publish this work, which was carried out in the course of an investigation of the general biology of fouling organisms. One of us (F. S. D.) was assisted by an expenses' grant from the Research Association, for which grateful acknowledgement is made. We should especially like to record our acknowledgement of the interest shown by Prof. J. E. Harris, Chairman of the Sub-Committee, and by the late Mr R. Elmhirst, Director of the Marine Station, Millport, in the progress of this work. We should also acknowledge the help of the Director of the Plymouth Marine Laboratory in providing a sample of *Tubularia larynx* for comparison with our own material.

SUMMARY

A description is given of a number of observations and experiments on the larvae and colonies of *Tubularia*. The experimental material could best be referred to the species *T. larynx* Ellis & Solander. Its characters are not wholly consistent with the diagnosis of this species, but the differences which exist are not great enough to warrant the erection of a new species.

Liberation of the actinulae takes place more freely in darkness than in light, and there is evidence which suggests that it only occurs in still water or in weak currents.

Immediately after liberation the body of the actinula is spherical and it rests on the tips of those aboral tentacles which point away from the mouth. Growth of the aboral region takes place and permanent attachment is possible when this region is long enough to come into contact with the substratum. This elongation takes place over a period of 24-48 hr. under laboratory conditions.

Temporary attachment can take place by means of the tips of the aboral tentacles; it seems likely that this is accomplished by the eversion of nematocysts.

A thin sheath of perisarc is present over the aboral region of the actinula when it is liberated. The perisarc is chitinous in nature, and permanent attachment is secured by means of an extra-chitinous cement, probably secreted by the glandular ectoderm of the aboral pole.

Exposure of the actinula larva to hypotonic sea water, low concentrations of copper and mercury and some organic compounds stimulates permanent attachment. These abnormal environmental conditions cause a decrease in the rigidity of the aboral tentacles; this allows the aboral pole of the larva to come into contact with the substratum prematurely.

Growth is rapid once permanent attachment has taken place. An extensive stolonial system is first established, followed by the production of a number

of stems and polyps. Gonophore buds appear on the primary polyp 2 days after settlement and some polyps can liberate actinulae 24 days after settlement. Most of the actinulae produced by a colony settle, if suitable substrata are available, in its immediate vicinity.

Only some of the polyps in any one colony liberate actinulae. Liberation continues for some days and is followed by autotomy of all the polyps in the colony. These are later replaced.

The biotic environment of the grown colony is briefly described.

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ON THE BIOLOGY OF THE SMALL COPEPODS IN LOCH STRIVEN

By S. M. Marshall, D.Sc.

From the Marine Station, Millport

(Text-figs. 1-32)

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INTRODUCTION

The importance of copepods in the economy of the sea is generally recognized, but our knowledge of their seasonal variations in breeding and growth is as yet very incomplete. The object of the present investigation is to study throughout a year the variations in the small copepods of Loch Striven in the Clyde sea area. Fortunately, the tow-nettings which had already been studied for *Calanus finmarchicus* (Marshall, Nicholls & Orr, 1934) were available and offered an opportunity of comparing the seasonal changes in the small copepods with those in *Calanus* and in the phytoplankton. The hauls were therefore re-examined and the small copepods picked out and separated into their developmental stages.

Details of the method of taking the hauls are given in the paper mentioned above. It is sufficient to say here that on each occasion five vertical hauls were taken with a modified Standard International Net of fine silk (200 meshes to the inch), and that from 27 March to 21 August inclusive one of the five was taken in two parts, the first from the bottom (60-70 m.) to 10 m., and the second from 10 m. to the surface. The five hauls were examined by eye, and if the four undivided hauls appeared to be similar they were mixed together; if one appeared decidedly different from the rest, it was kept separate and either

not counted, or its figures not included in the final estimate. The divided haul was of course always counted separately.

Figures and tables giving data for temperature and numbers of phytoplankton organisms on the dates when the hauls were taken are given in the paper cited above.

Methods of preservation, sampling and measurement were the same as described by Nicholls (1933) and Marshall (1933). In all but the first five stations where, for *Oithona*, only one-fifth of the catch was counted, the procedure was as follows. One-tenth of the catch was examined, and all stages of all copepods picked out. If the total number of any stage reached 100 in this tenth, it was not separated from the remaining nine-tenths of the catch. Subsequent tenths of the catch were examined and the other stages of the copepods picked out until a hundred of each stage had been separated from a known fraction of the catch or until the whole catch had been examined.

On a few occasions when the nauplii of a species were very numerous they were counted in one-twentieth of the catch. Winsor & Walford (1936) have shown that counting individuals beyond the number of 100 adds very little to the accuracy of the estimate of the population.

It frequently happened that the numbers in the divided haul were lower than those of the undivided haul average, and I am much indebted to Dr H. Barnes for studying the statistics of these variations in number. The results of his examination are not yet complete. However, it may be tentatively stated that there is considerable evidence that a proportion of the catch is lost in the divided hauls; this loss affects the numbers below 10 m. only. The loss was not constant throughout the season, but on occasion it was of the order of 50 % of the total catch below 10 m.

The figures for the vertical distribution determination have necessarily to be obtained from the counts of these divided hauls, and the actual proportions above and below the 10 m. level may therefore be subject to a variable error; qualitatively the seasonal changes are accurately represented.

When, according to the counts of *Calanus* already made by Dr A. G. Nicholls (1933), the divided and undivided hauls did not differ much, only the former was counted. This was so on ten dates between 27 March and 21 August; on twelve the undivided were also sampled and counted. In plotting the total numbers and percentage distribution of the stages (Figs. 1-14) throughout the season the estimates from the undivided hauls were used when available; those from the divided haul only are marked with an asterisk.

THE SPECIES AND THEIR REPRODUCTION

Nine species occurred in Loch Striven, six of them in abundance. *Pseudocalanus* and *Microcalanus* occurred throughout the year. Following With (1915) *Pseudocalanus minutus* (Krøyer) is taken to include *P. elongatus*, and *Microcalanus pygmaeus* G. O. Sars to include *M. pusillus* G. O. Sars.

Paracalanus parvus (Claus) occurred also, but, apart from nauplii of which a few were probably always present, not in numbers until July. Two species of *Centropages* occur. *C. hamatus* (Lilljeborg) was the common species; *C. typicus* Krøyer appears occasionally in the Clyde sea area, but it was not observed in the Loch Striven catches. *Temora longicornis* (Müller) and *Acartia clausi* Giesbrecht were the common representatives of their genera. *A. discaudata* (Giesbrecht) has been observed in the Clyde sea area, but not in Loch Striven.

Oithona similis Claus was the most abundant copepod and occurred the whole year round. This species is the one named by Sars (1918, p. 207) *O. similis* (emended from his description of it as *O. helgolandica* Claus (*ibid.*, p. 8)). There are slight discrepancies in the literature about the armature of the exopods of the swimming feet by which the species are distinguished, so the Loch Striven form was examined.

The exopods are three-segmented, and one of the distinguishing characters is the number of external spines and internal setae on the terminal segments of these exopods. In the key given by Wilson (1932, p. 311) the number of external spines on the terminal segments of the first four swimming feet in the female *O. similis* is said to be 2, 1, 1, 1, but in his description of *O. similis* on p. 314 it is given as 2, 1, 1, 0. Rosendorn (1927), in her study of the genus from the material of the *Valdivia* expedition, agrees with Wilson's key. Sars, in his description (1918, p. 8), mentions a spine on the terminal exopod segment of the fourth foot but does not show one in his figure (Pl. III, p. 4). In the Loch Striven specimens the number of external spines on the terminal exopod segments of the first three swimming feet is 2, 1, 1, and on the fourth there is, not a spine, but a fine seta which often lies close to the apical spine and is difficult to see.

Rosendorn gives the number of internal setae on this same terminal exopod segment as 5, 5, 5, 5, for the first four swimming feet, but Sars, in the figure already mentioned, shows only four on the first swimming foot and this agrees with the Loch Striven specimens.

Oithonina nana (Giesbrecht) also occurred; it was most common in February and March, decreased in April and almost disappeared during the summer. Its numbers began to rise again slightly in September and October. In the end of March and in April, when one haul was divided at 10 m., it was almost invariably found in the bottom part of the haul and might there be almost as numerous as *Oithona similis*, which at that time was concentrated in the top 10 m. The nauplii were not distinguished and the numbers of these given for *O. similis* probably include a small number of *Oithonina* nauplii, but even in February and March they were not numerous enough to affect the general result.

The nauplii of *Calanus*, *Pseudocalanus*, *Paracalanus* and *Microcalanus* are difficult to distinguish except by size. When only *Pseudocalanus* and *Micro-*

calanus were present their nauplii could be distinguished fairly easily, but when *Paracalanus* was present also it was much more difficult, and the numbers of nauplii are certainly less accurate than those for copepodites.

The five copepodite stages and the adults (male and female) were all separated, but the six nauplius stages of each species were lumped together. Copepods pass through the nauplius stages so quickly that since visits were made only once a week the proportions of the nauplius stages present could give no information about the development of broods.

The paper by Oberg (1906) was found very useful for identifying the nauplii and that by Kraefft (1910) for distinguishing the sexes of the copepodite stages.

Pseudocalanus minutus (Krøyer)

(Table III and Figs. 1 and 2)

The female does not normally develop a fifth leg, so the sexes can be distinguished easily in copepodite Stages IV and V. Occasional female specimens are found, both adult and Stages IV and V, which have a small fifth leg, but in such females the legs do not resemble those of the males, being smaller. Such specimens have already been described by With (1915). In the Loch Striven samples less than 1 % showed this abnormality (4 Stage IV, 13 Stage V, and 4 adult females).

The percentage distribution of the various stages is shown in Fig. 1 and the variation in total numbers in Fig. 2. It was not found possible to count the eggs in those species of copepod which do not carry an egg-sac, and, for the sake of uniformity, eggs are not shown in Fig. 1. As can be seen in Fig. 2, nauplii usually outnumbered eggs considerably, which is to be expected from the greater length of time (judging from *Calanus*) spent in the nauplius stages. During a good part of June and July, however, eggs were slightly more numerous than nauplii.

In the Fig. 1 type of diagram a developing brood is clearly indicated when the peaks for successive stages move to the right from bottom to top. The peaks for several developmental stages may occur on the same date, since the maximum abundance of any one stage is naturally often missed, but when all the peaks, or a majority of them, occur on the same date it indicates merely a sudden drop in the proportion of nauplii which is usually the most abundant stage.

In most Figures the times when diatoms were rich (arbitrarily fixed as over 100 cells/ml.) are marked along the foot of the diagrams by thick black lines.

When observations began in the middle of January, 50 % of the stock of *Pseudocalanus* consisted of Stage V copepodites, and almost all the rest was made up of eggs, nauplii and adults (Table III, Figs. 1, 2). During the next 4 weeks the Stage V moulted into adults, the females then spawned, and on

20 February over 80 % of the stock was present as eggs and nauplii (Fig. 1). These eggs and nauplii began to develop and the early copepodite stages became more numerous during February and March. From Fig. 1 it looks as

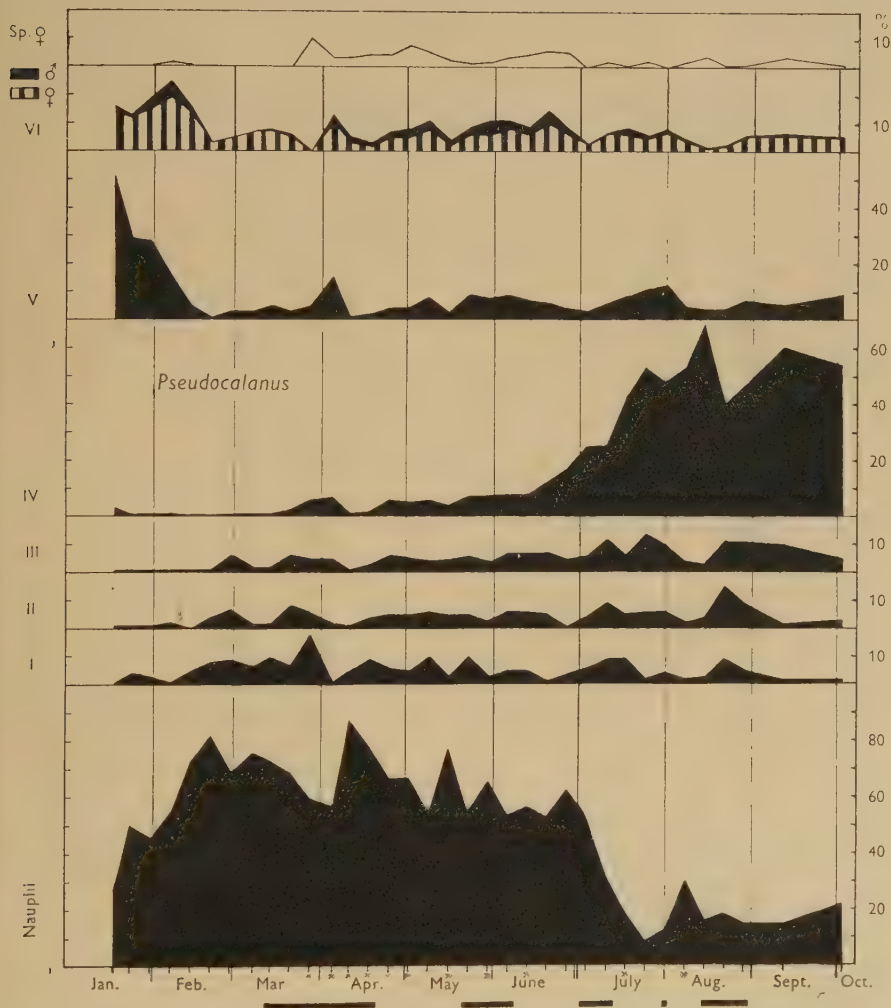


Fig. 1. *Pseudocalanus minutus*. Diagram showing the percentage of the developmental stages during the year. The percentage of adult females with spermatophores (*Sp. ♀*) is shown at the top. An asterisk indicates that counts were from a divided haul only (see p. 46). Periods of main diatom outbursts are marked by thick lines at the bottom of the Figure.

if the earlier nauplii of this brood did not complete their development, whereas the later nauplii did (Stage III appeared in numbers first on 27 February, Stage IV not till 4 April), becoming Stage V and adult about the beginning of April. It may be noted that the spring diatom increase began on 13 March

and would supply food for the later-produced nauplii and copepodites but not for the earlier. The actual numbers of the whole of this first brood were small, only a few hundred, and therefore it does not show on Fig. 2.

The adults of the beginning of April gave rise to another increase of nauplii in the middle of the month, whose development can be traced in the succeeding weeks. After this the percentage of nauplii remains high though variable, there are no distinct series of peaks on the curves for copepodite stages and breeding probably goes on continuously until July, when it falls off markedly.

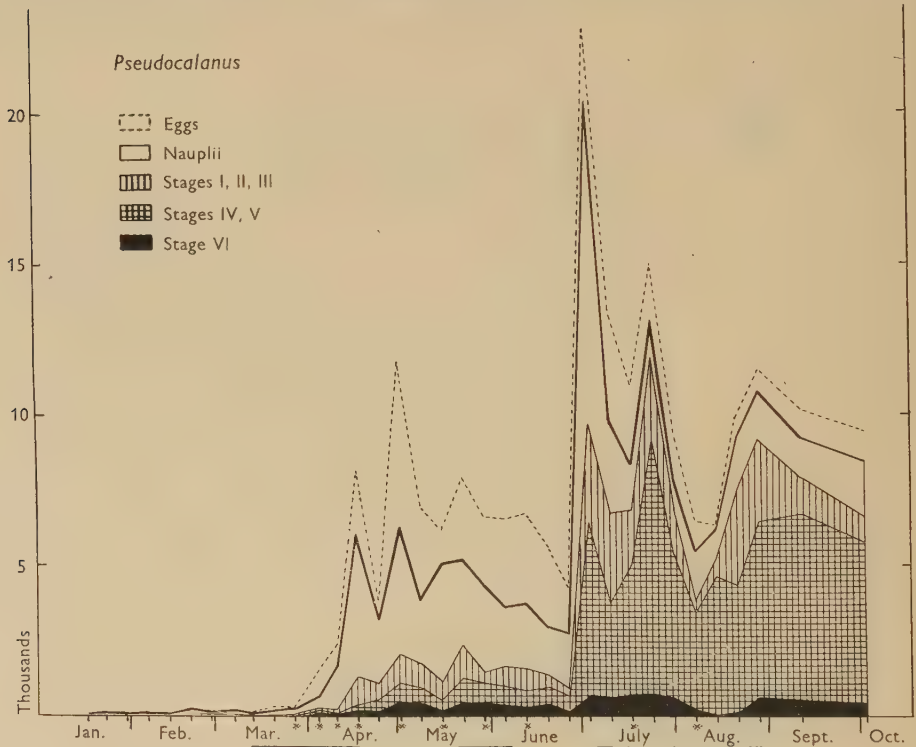


Fig. 2. *Pseudocalanus minutus*. Total number per haul throughout the year.

At the beginning of August there was a small but well-defined rise in the percentage of nauplii, followed a fortnight later by a rise in the percentage of early copepodites. This autumnal brood, however, does not get beyond Stage IV. Even from the beginning of July there was a very marked fall in the proportion of nauplii, and at the same time the number of Stage IV copepodites began to increase and continued to do so throughout the month and till the middle of August. From then till observations stopped at the beginning of October the proportion of Stage IV remained consistently high, usually between 40 and 60 % of the total catch. It is obvious that the majority of these copepodites

were not completing their development but were accumulating to form the autumn stock. In *Calanus* (Nicholls, 1933; Marshall *et al.*, 1934) the stock in autumn consisted almost entirely of Stage V, and later observations are required to find out when *Pseudocalanus* moults into Stage V and adult. As shown in Fig. 1 the change to Stage V had been completed by mid-January, and a certain proportion had even become adult by then.

The increase in total numbers (Fig. 2) is very marked with the arrival of the second brood in the middle of April, and there is another great increase to the maximum for the year at the beginning of July. The number of copepodites on 3 July does in fact seem greater than can be accounted for by the comparatively small number of nauplii in the two previous weeks, considering the natural mortality which must be taking place all the time. It is possibly an instance of the uneven distribution of plankton which must always be taken into account in this type of work. There is another increase in total numbers in the second half of August following the increase in nauplii then. It consisted mainly of copepodites, Stages I, II and III being abundant as well as IV.

The relation of the first brood to the spring diatom increase has already been pointed out. The April increase in copepod numbers came just at the end of this spring maximum, which, although it was much poorer than usual, continued for over a month. The second great increase in copepod numbers was accompanied by a shorter diatom maximum composed, like the spring one, of *Skeletonema costatum*. During the period when *Pseudocalanus* numbers were at their maximum there were several outbursts of diatom growth, although the predominant species were then *Chaetoceros* spp. and *Leptocylindrus* sp. On the other hand, a marked diatom maximum from 22 May to 5 June (again mainly *Skeletonema*) was not followed, as one might have expected, by an increase in copepods.

Pseudocalanus shows several interesting points both of resemblance to and of difference from *Calanus* in its breeding cycle. Both had a first brood, very small in numbers, beginning to develop in March about the time of the spring diatom increase. The next brood appeared earlier in *Pseudocalanus* than in *Calanus*, and whereas that of *Calanus* did not develop, that of *Pseudocalanus* did. It is possible that the diatoms, abundant in the first half of April only, may have accounted for this.

Calanus had much more distinct breeding periods than *Pseudocalanus*; between its successive broods egg production died away almost completely, whereas in *Pseudocalanus* the proportion of eggs and nauplii remained comparatively high till July and breeding and development were probably continuous. In *Pseudocalanus* the building up of a winter stock began in July, and it consisted in October of Stage IV; in *Calanus* the building up did not begin till mid-August and it passed the winter as Stage V.

In the Loch Striven hauls a number of *Pseudocalanus* eggs were found free, but the majority were in egg-sacs, most often attached to the genital segment

of the female. In the North Sea and English Channel, *Pseudocalanus* does not normally carry an egg-sac,* although two or three eggs are sometimes found attached to the genital segment. Fish (1936*b*) also states that in the Gulf of Maine the female is found only occasionally carrying two or three eggs. Sars (1903, Pl. X) figures the female *P. elongatus* with an egg-sac containing about seven or eight eggs and says in the text: 'Ovisac present of irregular rounded form but easily detached and containing a very limited number of ova.' In his figure of *P. gracilis* (Supplement, Pl. I), which, according to With (1915), is the same as *P. minutus*, the egg-sac is shown with twenty or more eggs. This variation in number is, however, within the range found in Loch Striven specimens. Females there were sometimes found with only two or three eggs attached, but it was assumed that these were in the act of laying, or had lost the main portion of the sac and they were counted as 'free' eggs.

Fish (1936*b*) says that to account for the large numbers of free eggs in the plankton each female must lay several hundred eggs. Since this seems, on the Loch Striven figures, too large a number for a single laying, each female may spawn several times, as has been suggested for *Calanus* (Marshall *et al.*, 1934).

The eggs in each egg-sac were counted throughout the year in order to estimate the average number laid by one female at a time and the seasonal variation. The average number varied considerably (Fig. 3), rising gradually from 9.5 on 13 February, to a maximum of 38.4 on 17 April. After this there was a gradual fall, interrupted by several very small increases, to a minimum of 8.0 on 11 September. The highest numbers occurred during the spring diatom increase and for a week or two afterwards; the slight interruptions of the downward curve are probably not significant, although they occur on, or just after, the dates of the secondary diatom maxima. It is not surprising that a well-fed copepod should produce more eggs than a starved one, but the variation seems to be dependent rather on the size of the female *Pseudocalanus*. The correlation between size of females (Fig. 16) and number of eggs is highly significant (0.98; 30 pairs of observations).

The free eggs were also counted and, assuming that the average number per egg-sac on each date holds for them also, it is possible to calculate the percentage of egg-bearing females present in any catch. This is a number, however, which shows violent fluctuations from week to week, and the variations do not seem to be related to any ascertainable factor. The maximum was 81 % on 12 June, a date on which the number of eggs, although high, was not at its maximum.

The number of females carrying spermatophores was also counted in a sample from each catch (that used for measurement) and is shown at the top of Fig. 1. The percentage was, with one exception, surprisingly low during the production of the first and second broods but was higher from April to June.

* Private communications from Mr R. S. Wimpenny, Lowestoft, and Mr P. S. B. Digby, Plymouth.

It was above 10 % only once, just before the appearance of the first brood females.

Males are usually much fewer than females in the catches, but this is probably because of their shorter life rather than because of any real discrepancy in actual numbers produced. When the proportions of the sexes are examined in copepodite Stages IV and V it is found that of the total number averaged over the year the percentage varies little from 50 % of each (Table I, p. 57). In the early part of the year, however (January to March), the proportion of males in Stage V is only 35 %, although slightly over 50 % in Stage IV. In several other species also males were scarcer during the early part of the year.

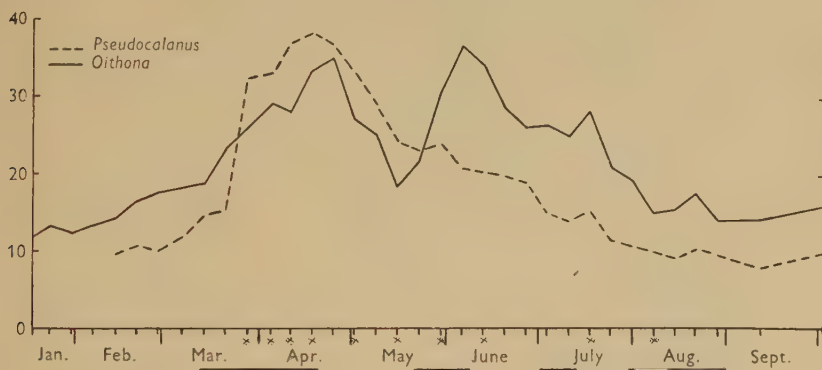


Fig. 3. Average number of eggs per female in *Pseudocalanus* and *Oithona*.

Paracalanus parvus (Claus)

(Table IV and Fig. 4)

Nauplii occurred throughout the year, but until July in small numbers only. Some of them were probably included among the *Microcalanus* nauplii, but they were separated from July onwards, and from the figures at that time it may be said that the percentage wrongly included is less than 10 and probably less than 5. Only an occasional copepodite stage was seen before the middle of July, but from then till 2 October, when observations stopped, they increased steadily (Fig. 4). The maximum total number (more than half nauplii) came on 31 August, but copepodites were at their maximum on 2 October. However, the decreasing proportion of nauplii and the fact that the majority were Stage V and IV indicates that reproduction was over for the season and that, like *Calanus* and *Pseudocalanus*, *Paracalanus* passes the winter in a late copepodite stage. No distinct broods can be made out and breeding was probably continuous during the period of observation.

The percentage of males was low, only 13.5 %. *Paracalanus* females, like those of *Pseudocalanus*, sometimes show abnormalities of the fifth leg. Several

specimens were seen in which it was four-segmented and not two-segmented as normally.

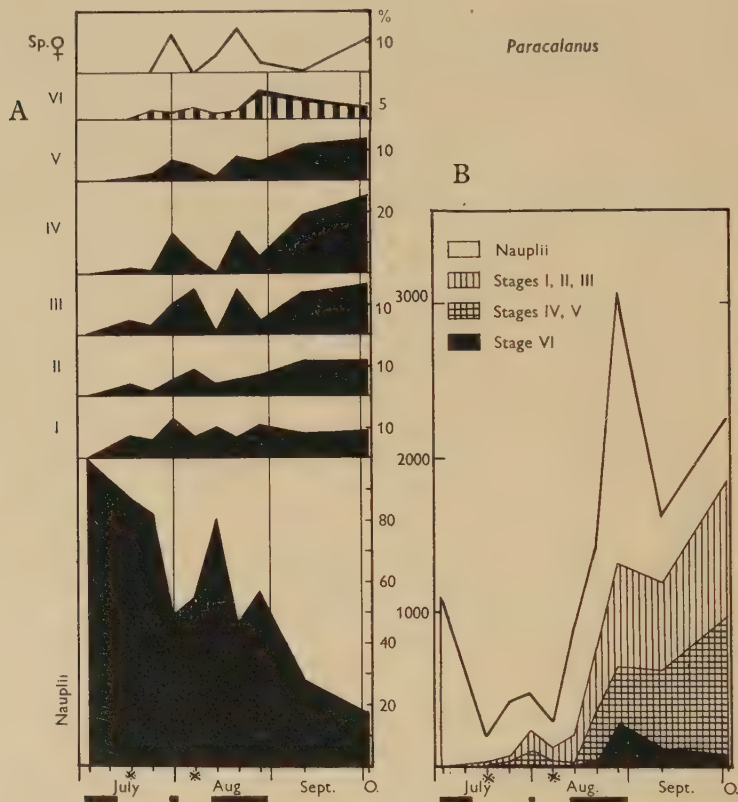


Fig. 4. *Paracalanus parvus*. A. Diagram showing the percentage of the developmental stages from July to October. The percentage of adult females with spermatophores is shown at the top. B. Total number per haul from July to October.

Microcalanus pygmaeus G. O. Sars

(Table V and Figs. 5 and 6)

This species differs from *Pseudocalanus* and *Paracalanus* and resembles *Calanus* in that it has well-marked breeding periods between which the proportion of nauplii and young stages falls to a low figure (Figs. 5, 6). It differs from all the other copepods studied in having its first breeding period well before the date of the spring diatom increase. When observations began (17 January) nauplii formed nearly 70 % of the catch, and the remaining 30 % was fairly evenly divided among all the copepodite stages. These nauplii, and the later nauplii found in February, grew up to adults during February and

March, and the second brood, beginning with a great increase in nauplii, came at the beginning of the spring diatom increase in March-April, and reached the adult stage in the beginning of May. Nauplii formed between 80 and 90 % of the catch during most of June; as in *Calanus* there seems to be a gap of several weeks between the time the adults appear and the time of

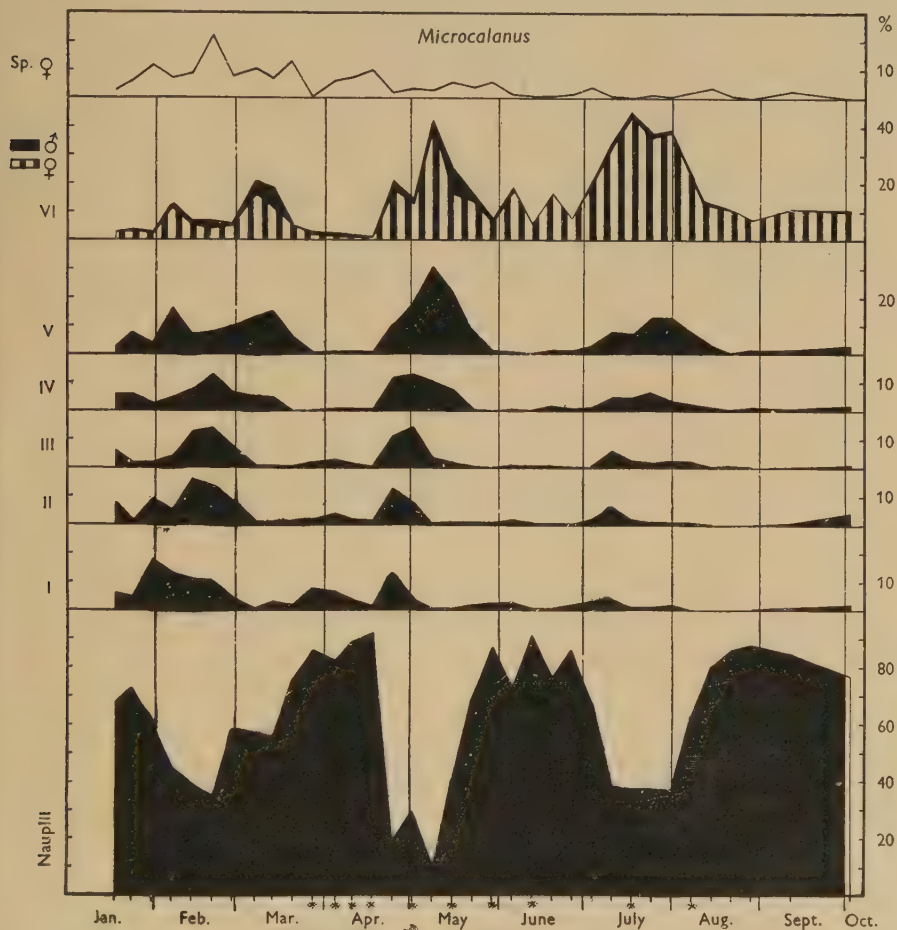


Fig. 5. *Microcalanus pygmaeus*. Diagram showing the percentage of the developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

maximum egg production as indicated by the number of nauplii; the eggs of this species were not counted. Diatoms were abundant at the end of May and again at the beginning of July, and it seemed to be mainly the later-produced of the June nauplii that grew up to form the third brood. The production of a brood in January, however, indicates that *Microcalanus* is less dependent on phytoplankton than the other species.

The July peak of adults was followed in the last half of August by another steep rise in nauplii, which, although the actual numbers were much lower than in summer, made up as large a proportion of the catch. When observations stopped in October nauplii were still the most abundant stage (77 %), with adult females next. This is a very different state of affairs from that found in *Calanus*, *Pseudocalanus* or *Paracalanus*, where the winter stock consisted mainly of copepodite Stages IV and V, and that stock was already built up by the end of August. It is possible either that *Microcalanus* went on breeding

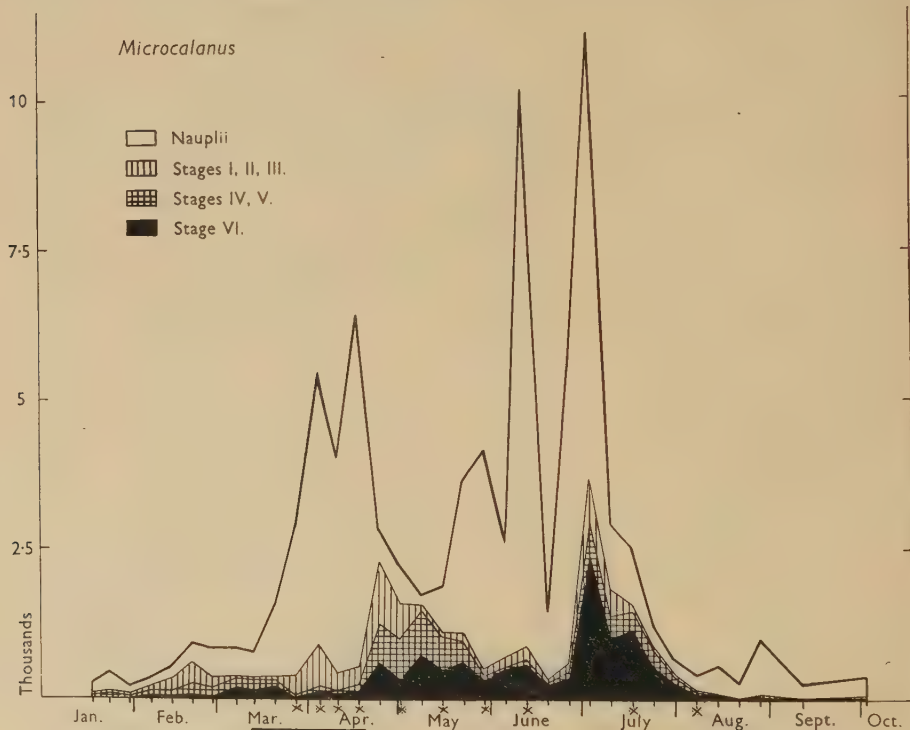


Fig. 6. *Microcalanus pygmaeus*. Total number per haul throughout the year.

at intervals throughout the winter, or that a winter stock of late copepodite stages was built up later in the year. Other possibilities are that *Microcalanus* passed the winter mainly in the nauplius or in the adult female stage. Observations during the winter are needed to decide which of these is correct.

On account of the very early first brood the total numbers of *Microcalanus* rose before any of the other copepods except *Oithona* became abundant. Already in February and the beginning of March the total number was nearly a thousand per haul compared with the two or three hundred *Pseudocalanus* present at that time. There were two maxima during the year, one in April, and one June to July, both consisting mainly of nauplii, but the second also

the maximum for copepodites and adults. The second and larger maximum was interrupted by a sharp fall in nauplius numbers on 19 and 26 June.

The relative proportions of the different stages showed some peculiarities. There was evidently a high mortality among nauplii, which is only to be expected and is shown in most copepods. From May onwards, however, the normal proportions of the copepodite stages were reversed, and the adult females and also Stage V were in general more numerous than the younger stages. Perhaps this indicates a longer life for females and Stage V than in the early part of the year, and gives some slight support to the suggestion that adult females may survive the winter. Adult males were always scarcer than females (although equally numerous in Stages IV and V) and became much more so after May. From January to May the percentage of males among the adults was about 23, from June to September it dropped to about 4 (Table I).

The proportion of females carrying spermatophores was highest in the early part of the year, but bore no apparent relation to broods (Fig. 5).

TABLE I. PERCENTAGE OF MALES PRESENT

Species	Stage IV	V	VI	VI	Ootten (1913)
	Jan.-Oct.	Jan.-Oct.	Jan.-Mar.	Jan.-Oct.	
<i>Calanus</i>	—	—	17·3	34·3	—
<i>Pseudocalanus</i>	47·7	50·2	11·1	23·1	18·3
<i>Paracalanus</i> *	45·0	40·3	—	13·5	16·4
<i>Microcalanus</i>	49·2	52·8	29·4	11·2	—
<i>Centropages</i>	—	56·1	—	63·8	20·7
<i>Temora</i>	49·9	55·7	—	57·8	20·7
<i>Acartia</i>	46·5	45·7	7·7	48·3	5·3†
<i>Oithona</i>	—	—	2·1	12·8	4·6

* In Loch Striven, from July to October only.

† *Acartia bifilosa*.

Centropages hamatus (Lilljeborg) and *Temora longicornis* (Müller)
(Tables VI and VII, Figs. 7-10)

Breeding is so similar in these two species that they may be taken together. From January until the middle of March the stock, apart from an occasional early copepodite, was represented entirely by nauplii. These were few in number, rising from 10 or 20 in January to 100 or 200 in March. In March copepodites appeared in numbers for the first time, a little earlier in *Temora* than in *Centropages*, and in the following weeks this first brood grew to maturity to reach the adult stage in April. It may be noted that the spring diatom increase began on 13 March and lasted till the middle of April. In the middle and second half of April, nauplii again predominated, and a second brood grew up during late April and May (*Temora*) or May (*Centropages*), reaching the adult stage about 10 and 22 May respectively. At this time diatoms were not abundant. Another great increase of nauplii in both species causing the maximum numbers of the year for *Centropages* (1900 per haul) coincided with the next diatom increase, but apparently no brood developed from these

nauplii. A marked increase in the proportion of adults in *Centropages* and of adults and copepodites in *Temora* on 19 June (Figs. 7, 9), seen in *Acartia* and *Oithona* also, was caused by a sudden drop in the number of nauplii, since the actual numbers of the older stages remained constant or even fell. The fourth

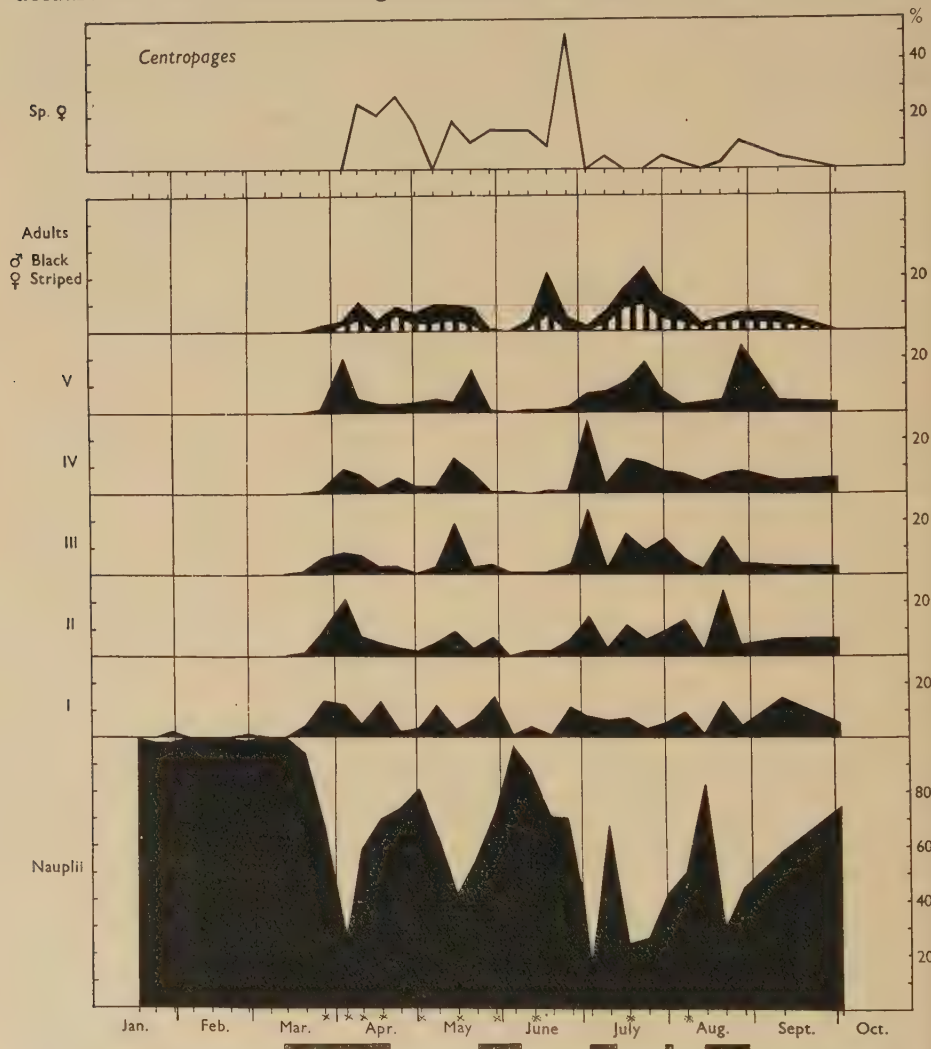


Fig. 7. *Centropages hamatus*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

brood, marked only in *Centropages*, developed from nauplii produced at the end of June, and during July and August breeding in both species seemed to be continuous. In *Centropages* the last distinct brood reached maturity at the end of August, and when observations stopped in October three-quarters of

the catch was nauplii and the remaining quarter was fairly evenly divided among Stages I–V. In *Temora* there was no distinct August brood, but in October the distribution was much the same as in *Centropages*, nearly 70 % of the stock being nauplii. This is a very different distribution from that found at the end of the winter, and it is possible that breeding can go on later in the year. Otten (1913), however, mentions that in his catches (in Kiel Bay) there were at the end of September and in November large numbers of *Centropages* nauplii with no corresponding copepodites. The nauplius seems an unlikely stage in which to pass the winter (cf., however, *Microcalanus*), and it is possible that adults survived in small numbers, living so near the bottom that the

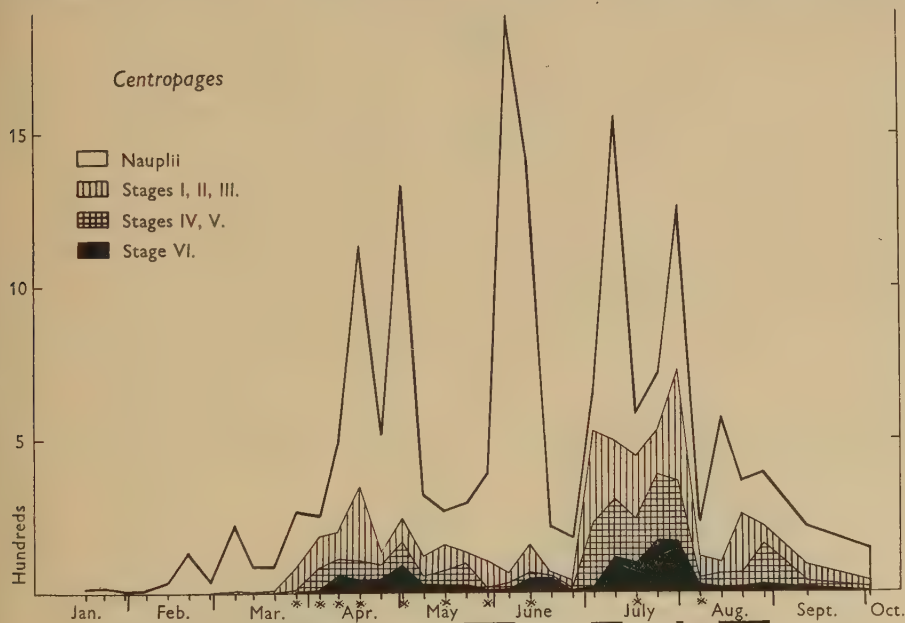


Fig. 8. *Centropages hamatus*. Total number per haul throughout the year.

vertical tow-net did not catch them, and producing a small number of eggs and nauplii throughout the winter. Another possibility is that some sort of resting egg is produced which can survive for long periods (see Fish & Johnson, 1937, p. 307).

Otten (1913) mentions *Temora* as carrying an egg-sac with four to eight eggs and says the sac breaks up readily. No sign of a sac was ever seen on the female *Temora* in Loch Striven.

Nauplii were responsible for most of the peaks in numbers during the summer (Figs. 8, 10), since they often formed over 70 % of the catch of *Centropages* and even more in *Temora*. In both species there were maxima of copepodites and adults in April at the time of the first brood and in July with

the third or fourth. In *Centropages* the numbers in July were the higher (700 copepodites and adults per haul on 31 July) and in *Temora* the April to May numbers (500 per haul on 1 May).

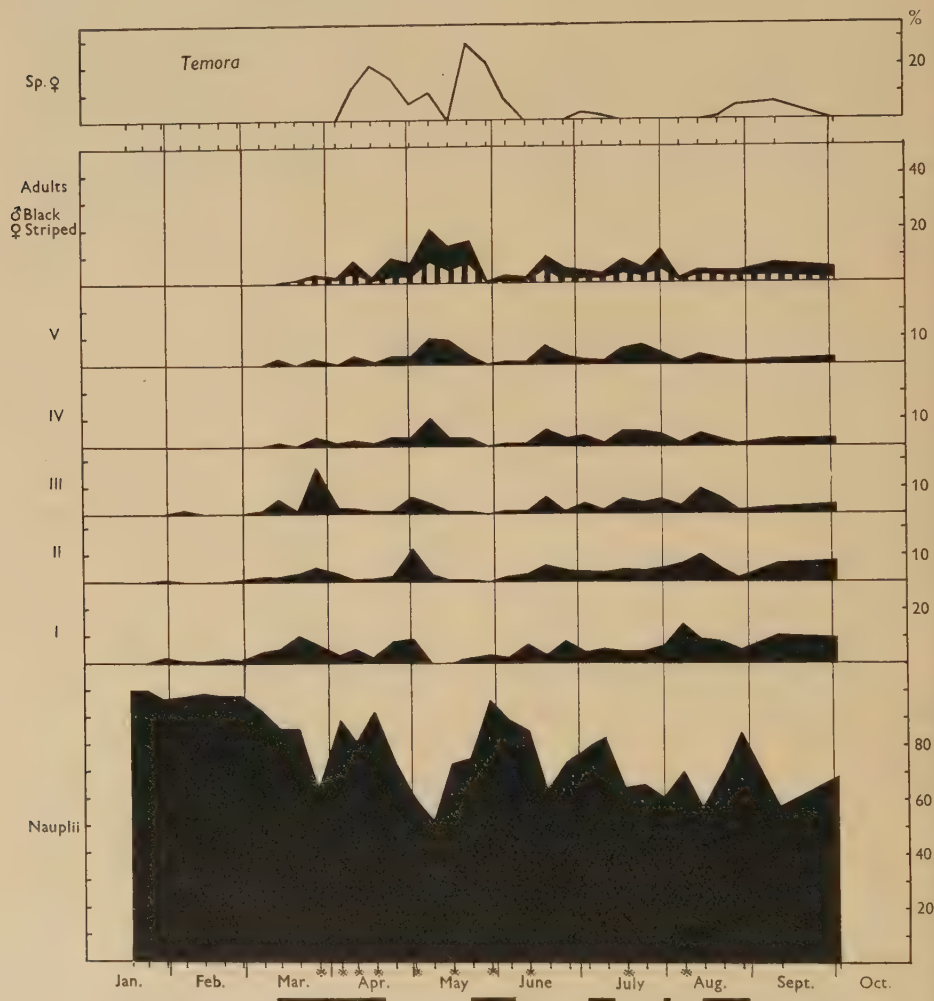


Fig. 9. *Temora longicornis*. Diagram showing the percentage of development stages during the year. The percentage of adult females with spermatophores is shown at the top.

Centropages and *Temora* differ from the other species of copepod examined in that males are more abundant than females throughout the year (Table I, p. 57). This was true also in the Nordåsvatn Fjord near Bergen (Wiborg, 1944). Even in Stage V there was a slight tendency for males to be more numerous. Taking the average over the year males formed 64 % of the *Centropages*

adults and 58 % of the *Temora* adults. In Stage V they formed 56 % in both species. In spite of this the number of females carrying spermatophores, although higher than in *Pseudocalanus* and *Microcalanus*, was lower than in *Acartia*, where the sexes were about equal, or in *Oithona* where males formed

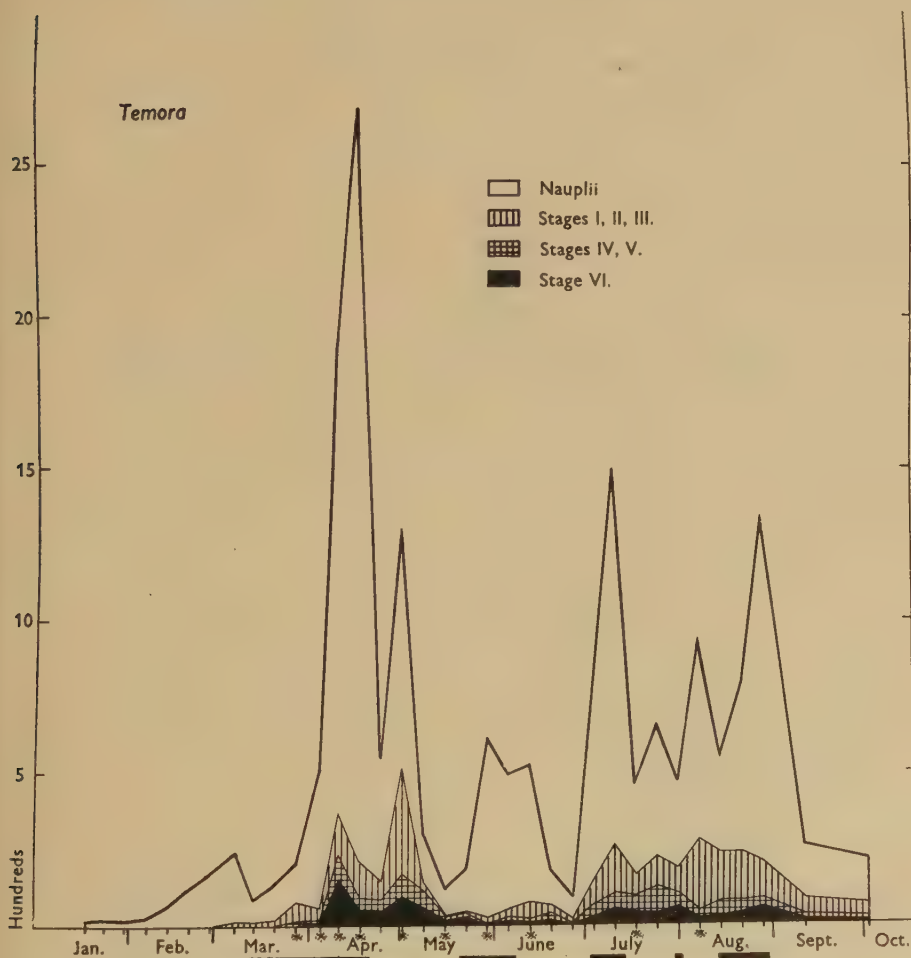


Fig. 10. *Temora longicornis*. Total number per haul throughout the year.

only 13 %. The number of spermatophore-bearing females is shown at the top of Figs. 7 and 9, and it is on the whole highest on the appearance of the first brood and varies irregularly throughout the summer. The peak in *Centropages* on 26 June means little, for only two females were caught, one with a spermatophore.

Acartia clausi Giesbrecht
(Table VIII, Figs. 11 and 12)

The stock of *Acartia* in January, unlike the other species examined, consisted almost entirely of adult females and nauplii. In February and March

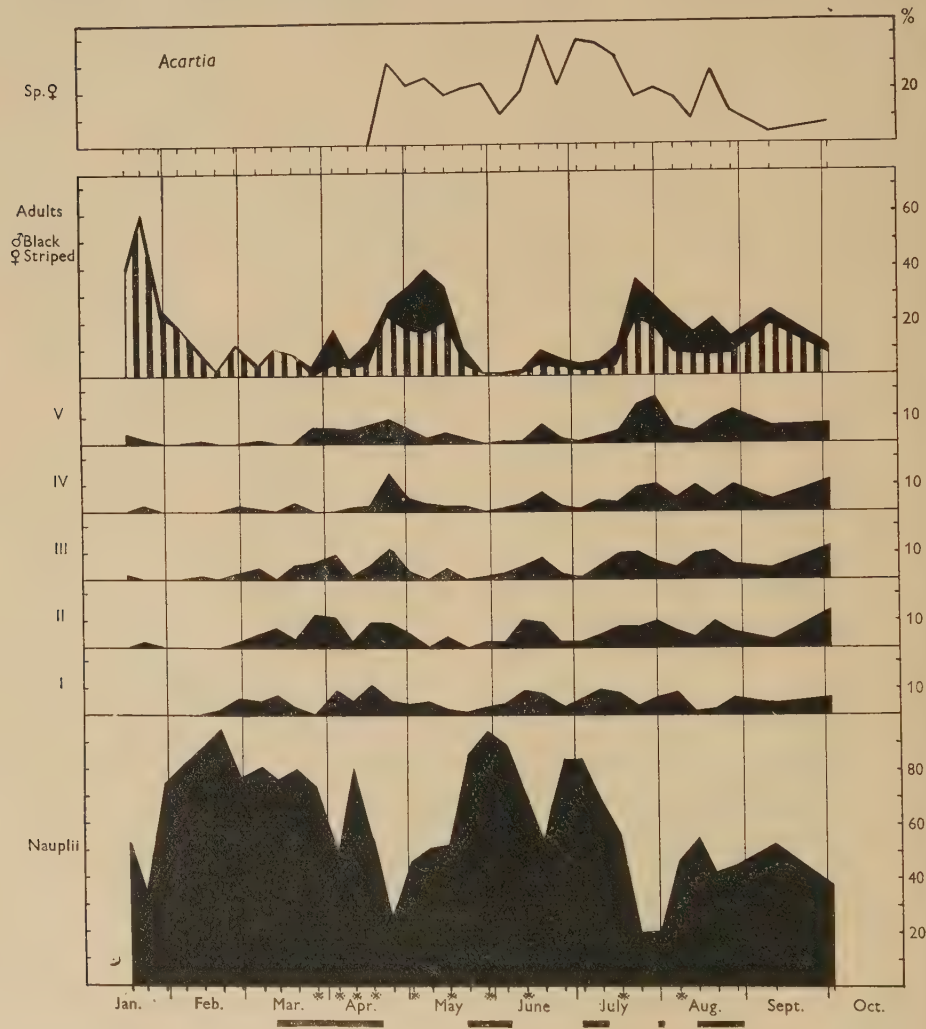


Fig. 11. *Acartia clausi*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

nauplii predominated, and in the latter half of March (along with the spring diatoms) the first brood grew up. The period of reproduction was rather spread out, or else there were two broods in close succession, of which the second

came to maturity at the beginning of May. The numbers at this time were, however, very small and hardly show in Fig. 12.

Another peak in nauplius production came with the diatom increase at the end of May, and this brood began to grow up during June. It is difficult to follow it to maturity, however, because of the sudden change (already mentioned) on 19 June in the proportions of nauplii and late copepodites.

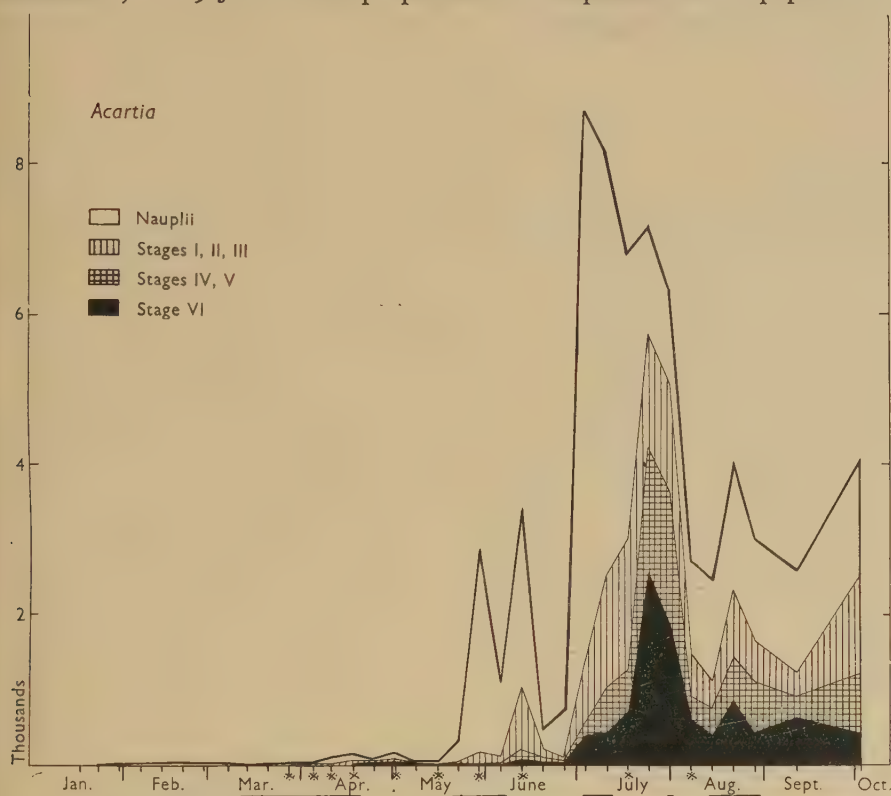


Fig. 12. *Acartia clausi*. Total number per haul throughout the year.

The peak in nauplius production at the beginning of July coincided with a diatom increase, and a brood, the third or fourth, developed during the month and reached the adult stage at the end of July and beginning of August. After this, breeding seemed to be continuous and the number of copepodites and adults remained high. When observations stopped in October there were less than 40 % of nauplii and the other 60 % was fairly evenly distributed among the different copepodite stages, so that in *Acartia*, too, it is possible that breeding may go on well into the winter.

The maximum number for the year occurred in July, as nauplii at the beginning of the month and as copepodites and adults (5000 per haul) at the end.

Taken over the year the sexes were almost equal in number in all stages where they are distinguishable (Table I, p. 57). Although among adults females predominated up to April and after August, during the summer months males often outnumbered females. There were no females carrying spermatophores in January and February, but from the end of April the number was high, especially during June and July, but it seemed to have no relation to the production of broods and only a slight relation to the predominance of males.

Oithona similis Claus

(Table IX and Figs. 13 and 14)

Oithona was the most numerous of the small copepods, and so, in spite of its small size, formed an important part of the plankton. A large proportion of the *Oithona* stock always consisted of eggs and nauplii; the mortality in these early stages must be very great. Until August the percentage of eggs and nauplii in the catch was always over 75 and often over 90. When eggs are omitted (so as to compare with the other copepods studied) the nauplii, except on three dates, formed more than half the catch.

In January, besides 60–70 % of nauplii the stock contained nearly 20 % of adults and a few copepodites of all stages, so that breeding may already have begun. These proportions remained very much the same until the end of March, when (at the same time as the spring diatoms) there was a rise in the percentage of nauplii and a distinct brood developed, reaching maturity at the end of April. An examination of the percentage size-frequency distribution curves (Fig. 29, p. 81) shows that the first large adult females of the spring brood began to appear as early as the end of March. From then till the end of April the curves are bimodal, with the number at the larger mode increasing until on 24 April and 1 May there were only large females present. These adults immediately produced another brood which grew up during May, but after this breeding was continuous. On 19 June there was the same abrupt rise in the percentage of adults and fall in that of nauplii as occurred in *Temora*, *Centropages* and *Acartia*. From July onwards the proportion of nauplii was lower than during the earlier part of the year. When observations stopped, adults and copepodites formed 60 % of the stock, and breeding may have continued throughout the winter.

Although *Oithona* was numerous throughout the year the numbers rose sharply only at the beginning of July, and the total stock (excluding eggs) on 3 July was 18,000 per haul. Numbers fell again to the beginning of August and then rose to the maximum for the year on 21 and 28 August when there were about 30,000 copepodites and nauplii, with 13,000 and 6000 eggs in successive weeks.

Males were always much scarcer than females, the discrepancy being most marked in early spring (Table I, p. 57). In January and March the males

numbered only 2 % of the adults, for the whole year 13 %. The number of females with spermatophores was about 10 % or less until April, but after this, with the higher proportion of males, it remained consistently high. The

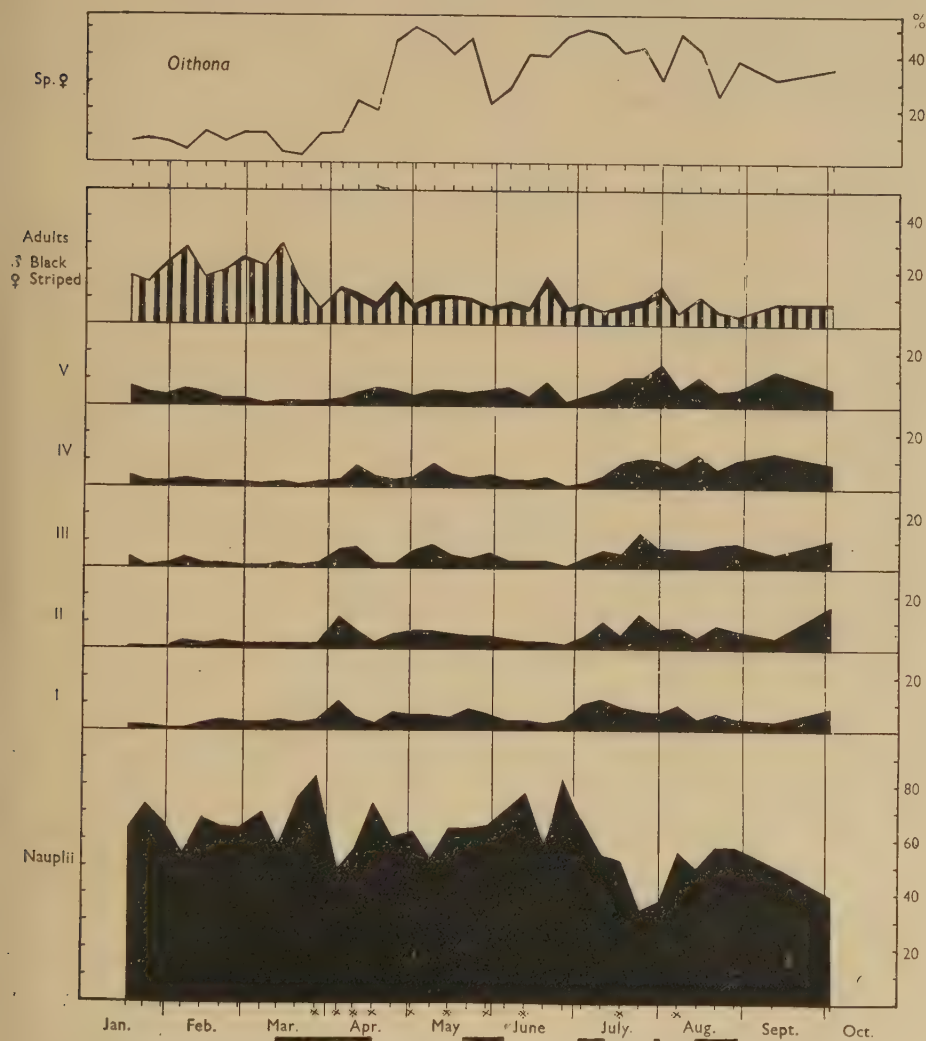


Fig. 13. *Oithona similis*. Diagram showing the percentage of developmental stages during the year. The percentage of adult females with spermatophores is shown at the top.

figure probably means little, however, for among the females carrying egg-sacs some had spermatophores and some had not (see p. 69).

The eggs are carried by the female in a pair of egg-sacs attached to the genital segment, so it is possible to count the number of eggs per sac and per

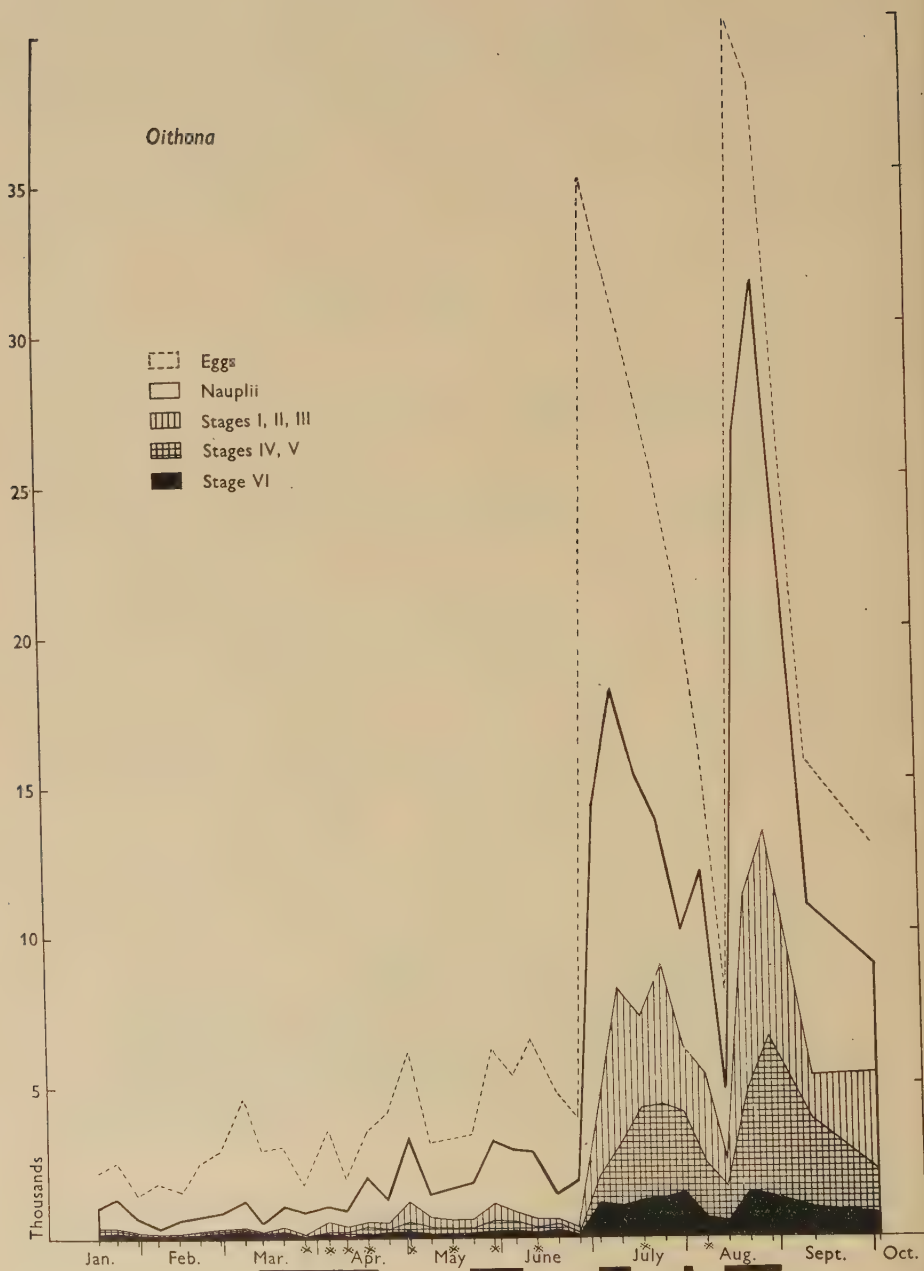


Fig. 14. *Oithona similis*. Total number per haul throughout the year.

female, and the latter is shown in Fig. 3 (p. 53). As in *Pseudocalanus* the number increased gradually to a maximum at the end of April, at the end of the spring diatom increase, when females were about their maximum size. There was then a rapid decrease in number until the middle of May, but from then till 5 June, unlike *Pseudocalanus*, there was a sharp rise to a second maximum. Thereafter numbers decreased gradually till the autumn, although there were two slight checks on the curve on the same dates as those found in *Pseudocalanus*.

The paired sacs did not always contain the same number of eggs, although they were usually nearly the same. The number per egg-sac varied from four to thirty-four, and almost the whole range might be covered in one catch. Over 100 egg-sacs were usually counted.

The curves indicate that the relation between number of eggs and size of female is less close than in *Pseudocalanus*, although the correlation coefficient is still highly significant (0.75, 35 pairs of observations). An examination of Figs. 3 and 28 shows that whereas egg numbers rose to a well-marked peak on 5 June the size of females showed only a slight rise at that time. Diatoms were abundant while the egg numbers were rising, and were scarce after 5 June, so that it is probable that the food supply has an effect on egg production. Diatoms were abundant also on the dates in July and August when the downward trend of egg number is checked, but the differences in egg number are not significant. Otten (1913) counted the number of eggs per sac and found that this varied throughout the year, being, like the nauplii, highest in April and October and lowest in August.

In considering the reproduction of the copepods as a whole, we can see that there are two types of breeding. In one the broods are distinctly separated by periods when eggs and nauplii are scarce. To this type belong *Calanus* and *Microcalanus*. In all the other copepods examined the broods were less distinctly separated and in the second half of the year were indistinguishable. In the second type there seems to be a shorter time between the appearance of adult females and the production of eggs and nauplii. In *Calanus* (Fish, 1936a; Marshall *et al.*, 1934) the maturing of the eggs is supposed to take about 3-4 weeks, and the same seems to be true of *Microcalanus*. In the other copepods a peak in nauplius numbers followed more closely (in two or three weeks) upon the appearance of adults, and two broods might appear in quick succession. In the late summer when breeding was continuous, no gap could be distinguished (see, however, Fish, 1936b, on *Pseudocalanus*).

In *Calanus* the time occupied in development from egg to adult was estimated, partly from the data from the Loch Striven hauls and partly from laboratory experiments, at about a month. There are no laboratory data for the small copepods, and since visits to the loch were made only weekly, estimates must be uncertain, but the time seems to be little shorter than in

Calanus. In most species the time from a peak in nauplius production to a peak of adults is 3-4 weeks. The great differences between spring and summer mentioned by Fish (1936c) do not occur here.

In all species the spring diatom increase seems to have had an important effect on reproduction. Although *Microcalanus* and possibly *Oithona* were breeding before it, yet during or at the end of the diatom-rich period (which in 1933 was long-drawn out—13 March to 17 April), every species showed an increase, in most of nauplii, and in all a successive development of early and late copepodites and adults. The date varied from one species to another between the middle of March and the middle of April. In *Pseudocalanus* and *Acartia* the actual numbers of the first brood were very small; in *Microcalanus*, *Centropages* and *Temora* they were considerable, especially when compared with the numbers occurring later in the year. In all species nauplii form a large proportion of almost every catch, and the greatest mortality must take place at this early stage. Fish (1936a, b) suggests that another dangerous period in the life of a copepod is during the maturing of the eggs, and that in *Calanus* the mortality is actually greatest at that stage, and is important also in *Pseudocalanus*.

The maximum number of all species of copepod except *Temora*, and sometimes *Calanus* (Nicholls, 1933), came during the summer, in July or August, but the date varied from species to species. This was true for the maximum numbers both of nauplii, and of copepodites and adults, which in *Microcalanus* and *Oithona* occurred on the same date. Besides this summer maximum there was usually a secondary maximum earlier in the year, in April or May, but this was smaller and more variable. In *Acartia* and *Oithona* it was small, in *Temora* it was more important than the summer maximum.

The proportion of the sexes varied among the different species, and it varies also from place to place. Otten (1913) gives figures for seven copepods (Table I, p. 57), mostly the same species as those in Loch Striven, but in his samples males were much scarcer. In both places, however, *Oithona* had the smallest, and *Centropages* and *Temora* the highest, proportion.

In Loch Striven (Table I) the percentage of males in *Calanus*, *Pseudocalanus*, *Acartia* and *Oithona* was lowest from January to March. In *Calanus* and *Pseudocalanus* it was highest from April to June, but in *Acartia* and *Oithona* the proportion did not vary much from April onwards. *Centropages* and *Temora* were too scarce before April for the number of males to be reliable, and after April the proportion remained fairly constant. In *Microcalanus*, on the other hand, their percentage was highest in April and was very low after June.

If, as seems most probable, these very varying proportions indicate the length of life of the adult, then in some species the female is the longer lived, in others the male. The length of life also varies at different times of the year, and this we already know to be true of some of the earlier stages such as Stages IV and V of the autumn stock of *Calanus*, *Pseudocalanus* and *Paracalanus*.

In *Calanus* (Marshall *et al.*, 1934) the percentage of adult females carrying spermatophores was highest before the production of each brood of eggs, and it was observed that the spermatophore was usually lost before the eggs were ripe for spawning. No such relation was made out in the small copepods. In one species (*Oithona similis*) the spermatophore was often retained even after the eggs had been spawned, and this may be so in other species also. It is curious, too, that the very varying proportion of males seems to have little influence on the number of females carrying spermatophores.

VERTICAL DISTRIBUTION

From 27 March to 21 August one of the five hauls was taken in two parts, from the bottom (60–70 m.) to 10 m., and from 10 m. to the surface. It must, however, be remembered (see p. 46) that there may have been a considerable and variable loss from the bottom haul which means that the proportion of copepods below 10 m. may be greater than appears from the figures. It is felt that despite this disadvantage the results obtained are substantially true.

In Fig. 15 is shown for all stages of each species the percentage above and below 10 m. No allowance has been made for the much greater depth of water sampled below 10 m. It is felt that the copepods are very unlikely to be evenly distributed throughout the column, and there are in fact indications that they may have been confined to the top 20 or 30 m. A series of samples taken at 10 m. intervals from top to bottom would give a truer picture of their distribution.

It will be seen that from the end of March till the middle of June the great majority of all stages of all species except *Microcalanus* was above 10 m. There was then a rapid descent, and in July most stages of all species were wholly or largely below 10 m. In August there was a gradual rise again in most species, more marked in the younger stages, but when observations stopped on 21 August the distribution had not yet returned to the state shown at the end of March.

Although this gives a general picture of the copepod distribution, there was considerable variation in detail between the different species and the different stages of the same species. *Microcalanus* was unlike any of the others, since during almost the whole year all stages remained consistently below 10 m. On 22 and 29 May the proportion of Stages II and III above 10 m. increased, but the numbers then present were too small to be significant, and on the last two dates in August Stages I and II were absent altogether. The rise of the nauplii in August, however, was based on considerable numbers and seems to be real. On the first two dates, 27 March and 4 April, a considerable proportion of all stages except males and nauplii was found above 10 m., and this may mean that there is a period during the winter when *Microcalanus*, like the other copepods, lives mostly near the surface. Further observations are needed to

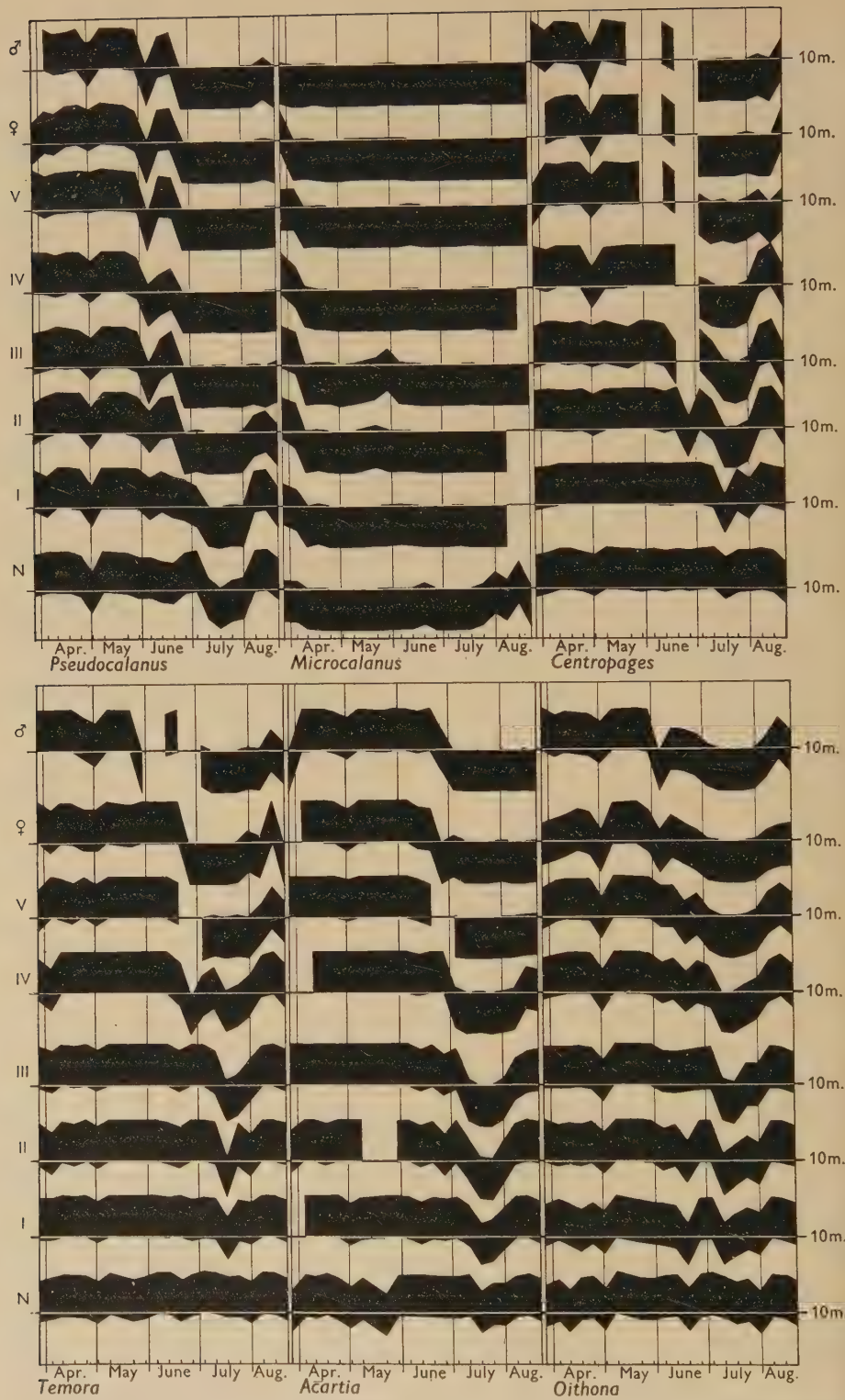


Fig. 15. Diagram showing the percentage of copepods above and below 10 m. from 27 March to 21 August. The nauplii and copepodite Stages I-VI are shown separately for each species.

decide the point, but it may be noted that off East Greenland (Ussing, 1938) *Microcalanus*, like most other species, is found near the surface in winter and in deep water in summer.

In *Calanus* (Marshall *et al.* 1934) the adults and Stage V went below 10 m. in the beginning of June, and the earlier copepodites not till the beginning of July. In the adults and Stage V of this species it was therefore those of the first brood only which were found above 10 m. All stages stayed mainly below 10 m. until observations ended on 21 August.

In *Pseudocalanus* and *Acartia* the return to the surface in August did not take place in the older stages. In *Pseudocalanus* all stages from adults down to Stage III, and in *Acartia* adults and Stage V remained below 10 m. until observations stopped. In the younger stages the descent in July lasted for a shorter time, and there was a gradual rise again during August. The nauplii of *Acartia*, indeed, remained largely above 10 m. all the time.

Centropages and *Temora* resembled each other closely, and although the course of events was the same the descent in July was in general less marked than in the other copepods. Numbers in June were too low to give a reliable estimate for the adults and older copepodites, but all were below 10 m. by the beginning of July. The younger stages went down later and rose earlier and the nauplii showed little change at all. A considerable proportion even of adults had risen to the surface again in August.

Oithona showed the same changes, but in even less degree. There were few dates on which copepodite Stages I and II were mostly below 10 m., and in August the adults and older copepodites were again mainly above 10 m.

All copepods but *Microcalanus*, then, showed the same series of changes, but the younger the stage the less marked the descent into deeper water and the more rapid the subsequent rise. Among nauplii only *Pseudocalanus* showed a clear migration downwards, and in *Temora* and *Oithona* the descent was little marked even in Stages I and II. The time of descent did not correspond to the presence of any particular brood except in *Calanus*.

Since this summer migration occurs in so many species of copepod there is probably some environmental factor causing it. Fish (1936*b*) says that in the Gulf of Maine *Pseudocalanus* disappears from the inshore waters in June and July when the temperature rises above 15 or 20°C., and is found in colder bottom water during the summer. In Loch Striven the temperature never rose much above 15°C. and that not till the end of July, but it is possible that the downward migration may have been caused by increasing warmth. Ussing (1938) attributes the migration to light, and this, too, may have been a factor in Loch Striven.

Apart from this seasonal retreat into deeper water there were several days on which there was a sudden increase of the copepods below 10 m. Such dates were 1 May, 5 June and possibly 21 August. The sudden dip is not seen in the

curves for all species or all stages, but it is apparent in many, most clearly in *Pseudocalanus* and *Oithona*, so that these descents also had probably some common environmental cause. They cannot be accounted for by the weather on these particular days, for although 1 May was bright with high cloud, 5 June and 21 August were overcast and rainy.

It is possible that water movement caused by wind was responsible. Such movements may go on for several days after the wind which caused them has died away. The abrupt temperature fluctuations shown in May and June (Marshall *et al.*, 1934, Fig. 5, p. 804) at the surface, and occasionally even at 30 m. (the only depths where temperatures were measured), support this suggestion, and the fact that such migrations are shown in almost all stages of development, even when the temperature change does not go as deep as 30 m., suggests that the population was living above this depth. In the marked disturbance of distribution shown on 5 June the nauplii and young copepodites were less affected than the old, perhaps because they were living nearer the surface.

SIZE

The size of the six species of copepod from copepodite Stage III upwards was measured every week when available. When possible samples of about 100 were used, but the number was often lower, especially in *Centropages* and *Temora*. The measurement used was that of the cephalothorax except in *Oithona*, where it was taken from the tip of the cephalothorax to the end of the first abdominal segment. This was to make the measurement comparable with that of the other copepods, since in Cyclopidae the 'joint' comes between the first and second abdominal segments. The results are shown in Tables X–XVII and Figs. 16–29. Figs. 16, 18, 20, 22, 24, 26 and 28 show the median length throughout the year, Figs. 17, 19, 21, 23, 25, 27 and 29 the percentage size-frequency distribution. For economy of space the latter is not shown for every week but only for a selected number of dates.

All measurements were made with an ocular micrometer whose divisions equalled $17.4\ \mu$. Those between two divisions were taken at the lower figure. In Tables X–XVII the measurements have, for economy in space, been grouped either in twos (for the smaller copepods *Microcalanus*, *Paracalanus* and *Oithona*) or in threes (for *Pseudocalanus*, *Centropages*, *Temora* and *Acartia*), so that each column corresponds to a size difference of 35 or of $52\ \mu$. Figs. 16–29 have, however, been prepared from the extended series of measurements.

Sex differences. The size relationship between the sexes differs considerably in the different species of copepod. Normally the female is the larger, both when adult and in those copepodite stages where the sexes can be distinguished, although in Stage IV the difference is often negligible. This is so in *Calanus* and *Oithona* (where the sex can be distinguished only in the adult), and also in *Centropages*, *Temora* and *Acartia*.

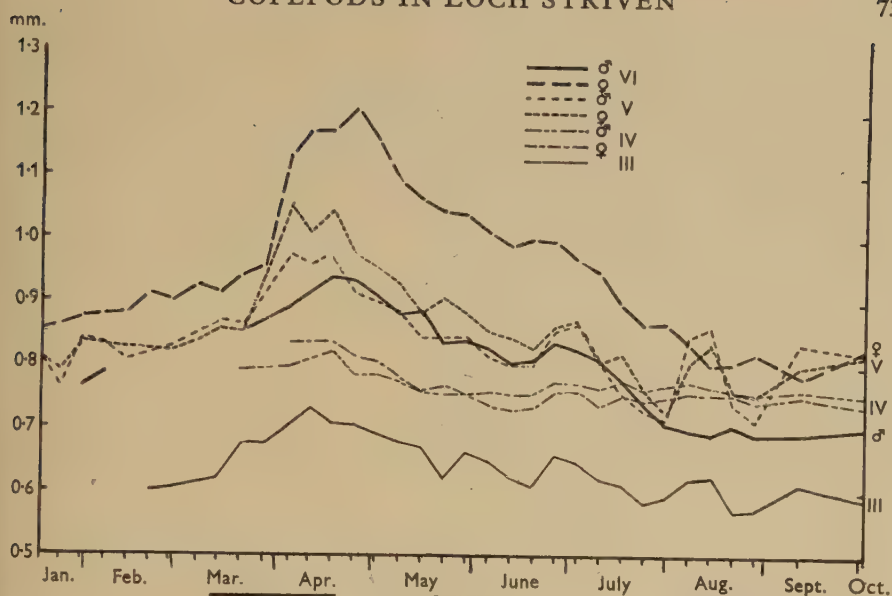


Fig. 16. *Pseudocalanus minutus*. Median size of copepodite Stages III-VI throughout the year

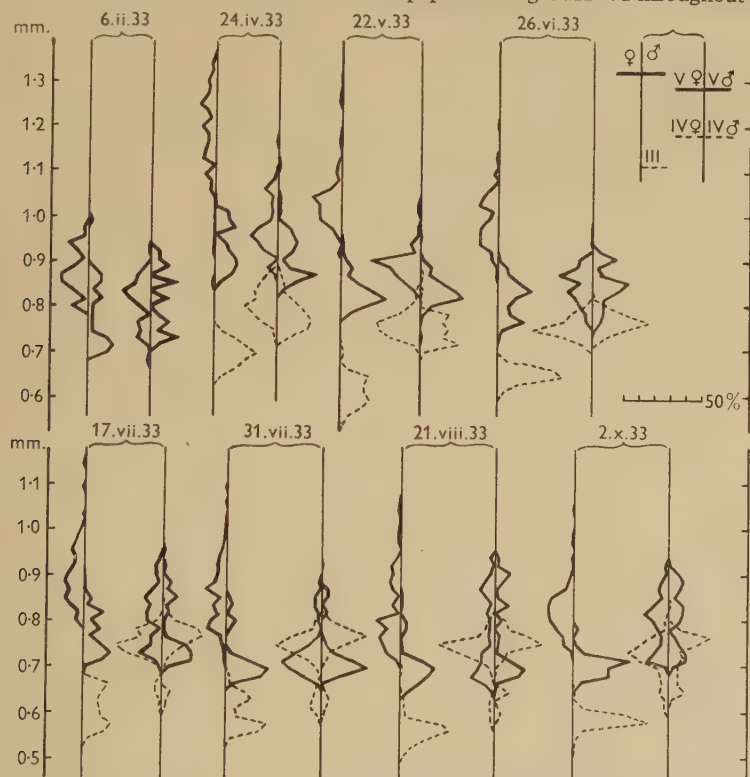


Fig. 17. *Pseudocalanus minutus*. Percentage size distribution of Stages III-VI on selected dates.

Sizes in *Pseudocalanus* (Table X, Figs. 16, 17) were normal in so far as the adult female was larger than the adult male, and the Stage V female usually larger than the Stage V male. In Stage IV there was little difference in size between the sexes, and the female was larger during the early part of the year, the male during the later. The adult male was, however, only about the same size as the Stage V male, and until August the two curves for median size (Fig. 16) cross and recross one another. After August it is smaller still and well below the median size of even the Stage IV. From August onwards, indeed, the median size curves are very much mixed up; Stage V is sometimes larger and sometimes smaller than Stage IV, and even the adult female is on some dates smaller than the Stage V. This can be partly explained by the breeding conditions. At this time Stage IV made up 40-60 % of the total population; this stock did not continue its development, and any small alterations caused by the addition of copepods from Stage III, or loss by moulting into Stage V, could make little difference to the median size, which remained almost constant from July onwards. If the size-frequency distribution curves for Stage V (Fig. 17) are examined, it can be seen that in August the total range in size is very great and that there is a group of large and of small Stage V in both male and female. On some dates most of the Stage V are in the large group and on others mostly in the small. This accounts for the very irregular median-size curve in Stage V.

During August the range of size as well as the mode was smaller in the adult male than in Stage V, and it seems probable that in the final moult the male alters little in size if it does not actually decrease. Experimental work on living copepods is needed to confirm this.

The observations in Loch Striven agree with those of Kraefft (1910), who made a few measurements of *Pseudocalanus* in Kiel Bay and found that the male was larger than the female in Stage IV (like the Loch Striven samples in late summer) but smaller in Stage V and much smaller in the adult.

In *Microcalanus* (Table XII and Figs. 20, 21) the adult female was larger than the male during most of the year, but in both Stages V and IV the male is larger than the female, so that whereas in its three final moults the female increases by much the same amount, in the male there are two large increases followed by a very small one. The growth factors (ratio of the size before and after moult) were respectively:

1.14, 1.17, 1.15; 1.22, 1.20, 1.04.

Paracalanus (Table XI, Figs. 18, 19), which was numerous enough to measure only from July onwards, has gone even further from the normal, and in these samples the male was larger in Stages IV, V and VI, and even the Stage V male was larger than the adult female. Kraefft (1910) shows a similar relationship in his diagram based on measurements in February and August; the male is larger than the female in Stages IV, V and VI, but the Stage V male is much the same size as the adult female.

Seasonal change. Apart from these minor sex differences the size of all the copepods showed a seasonal change. Comparatively small in winter, the size of all stages, especially the adults, underwent a great and rapid increase in spring to a maximum sometime in April, and there was then a gradual decline until August. After this there was in most species little further change, and the sizes were much the same as those found in January.

Since *Paracalanus* copepodites (Table XI and Figs. 18, 19) did not appear in numbers till July, it cannot be known whether it conformed to this normal

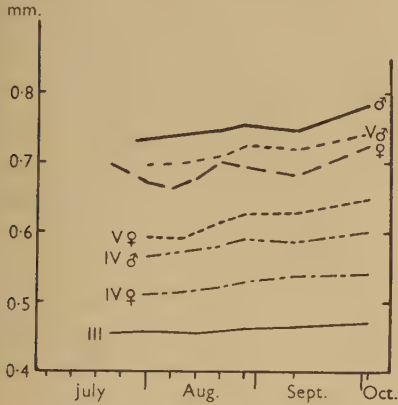


Fig. 18.

Fig. 18. *Paracalanus parvus*. Median size of copepodite Stages III-VI from July to October. Lines as in Fig. 16.

Fig. 19. *Paracalanus parvus*. Percentage size distribution of Stages III-VI on selected dates.

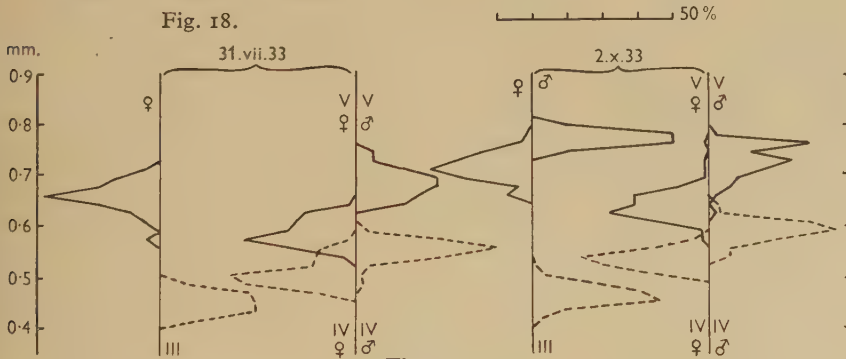


Fig. 19.

type early in the year. From July to October the curves for median size are very regular with a slight tendency to rise. The curves for *Microcalanus* are also very regular and show only minor variations. In all copepodite stages they rise gently to a maximum, which lasts most of April, and then decline gently during the rest of the year.

In *Pseudocalanus* (Table X and Figs. 16, 17) the increase in size in spring was much more abrupt, and there is a well-marked maximum occurring on 10 April in Stage III and on 24 April in females. After April there was a more gradual decrease till the autumn, with only minor, and probably not significant, fluctuations. One of the most striking features was the wide range in

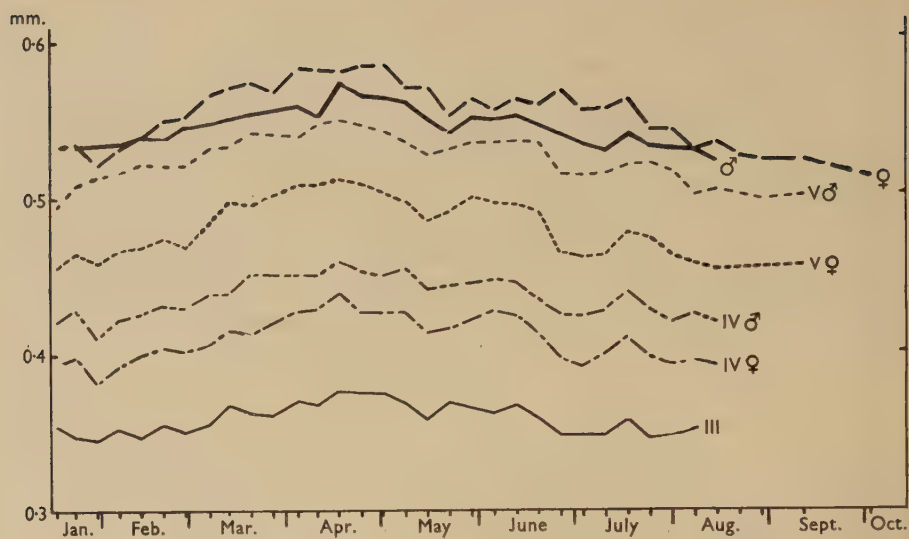


Fig. 20. *Microcalanus pygmaeus*. Median sizes of copepodite Stages III-VI throughout the year. Lines as in Fig. 16.

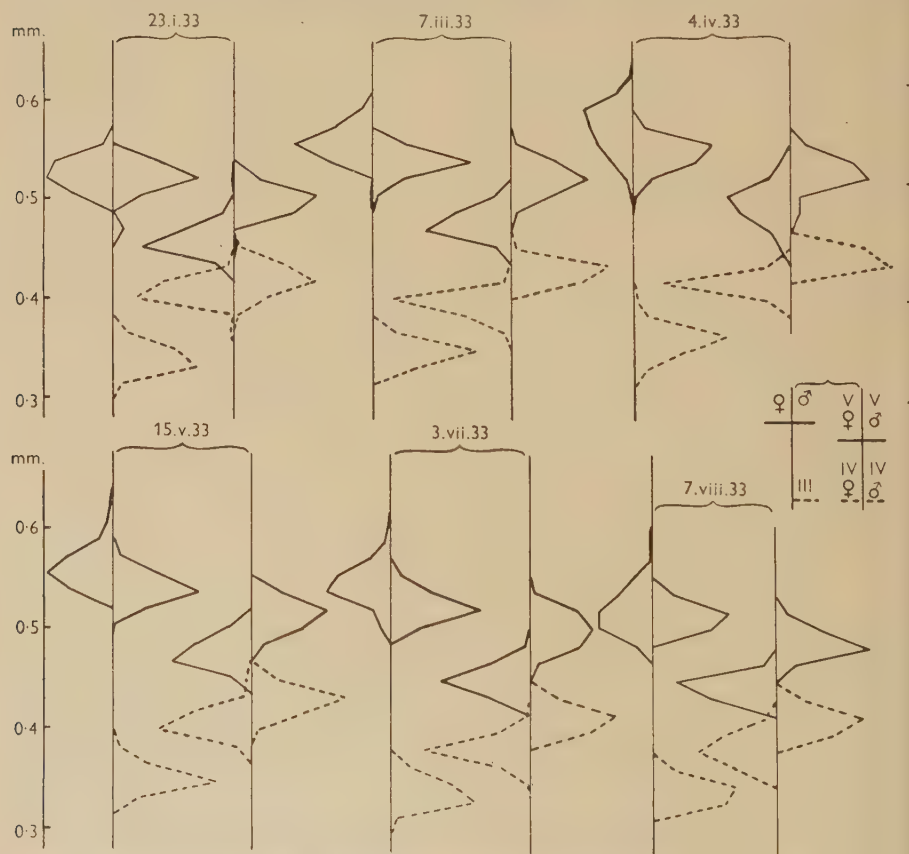


Fig. 21. *Microcalanus pygmaeus*. Percentage size distribution of Stages III-VI on selected dates.

size, so that each stage overlapped the next, sometimes to a considerable extent. Except in Stage III the curves of Fig. 17 are rarely unimodal, and for the older stages are multimodal or very irregular. The two modes seen in Stage III curves do not correspond to the differences in size between male and female Stage IV. Störmer (1929) refers to the great range in size of *Pseudocalanus*, and the samples of Adler & Jespersen (1920) show a maximum size range very much the same as that of the females in Loch Striven.

In *Calanus* with the appearance of a new brood, the size-distribution curves usually became more compact and unimodal as if a large number of similar individuals had moulted together; the median size often showed a rise also (Marshall *et al.*, 1934). In *Pseudocalanus*, however, with its more continuous breeding, this was not obvious. Stage III showed a clearly unimodal curve on its first appearance with the first brood at the end of February, and again at the end of April, May, June and August, perhaps corresponding to broods, but the later stages did not do so regularly. From July onwards, as might be expected from the building up of a large stock which did not develop beyond Stage IV, the curves for Stage IV became more uniform, showing one distinct mode (a little smaller in the female than in the male), with occasionally a smaller size group, perhaps of later-moulting animals.

In *Centropages* and *Temora* (Tables XIII, XIV and Figs. 22–25) there were not enough copepods to measure in the early part of the year, but there was a very well-marked size maximum in the later stages of both species on 24 April. The subsequent decline to a minimum in August was interrupted in both species by a smaller increase in size on 19 June, marked only in adults in *Temora*, but also in Stage V in *Centropages*. *Temora* females, although few in number, also showed a decided increase on 15 May, which was the approximate date of appearance of the adults of the second brood. On 19 June, however, there is nothing obvious in either species to account for an increase in size. The numbers of all stages measured (except males) were small, and the change was perhaps not significant. The size of all stages reached a minimum in the end of July or beginning of August and thereafter began to rise again gradually. After 11 September there were too few to measure. An autumn size-maximum has been described for *Temora* by Adler & Jespersen (1920). In both *Centropages* and *Temora* the range in size of the different stages, distinct during the early part of the year, came to overlap more and more in late summer (Figs. 23, 25).

Apart from a few females in January and February, *Acartia* (Table XV and Figs. 26, 27) was too scarce to measure until 24 April or later, but it seems fair to assume that during March and April the size was gradually increasing and that it reached its maximum about 24 April, a date which marked the first appearance of the spring brood. There was a steady decline from then till the beginning of August, after which the size remained pretty constant or rose a little. Stages V and III were present only in very small numbers at the



Fig. 22. *Centropages hamatus*. Median size of copepodite Stages III-VI throughout the year. Lines as in Fig. 16.

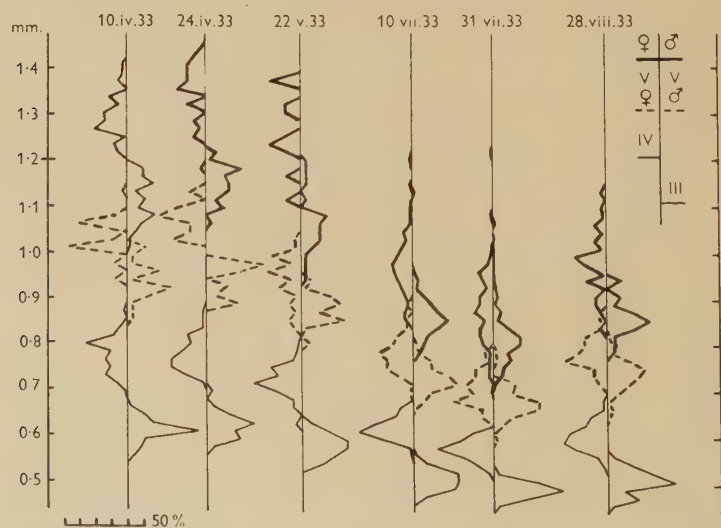


Fig. 23. *Centropages hamatus*. Percentage size distribution of Stages III-VI on selected dates.

end of April, and their maximum size is therefore unknown. *Acartia* differs very much from the other copepods in its size-frequency distribution curves (Fig. 27), for these are almost always clearly unimodal, and the range of size

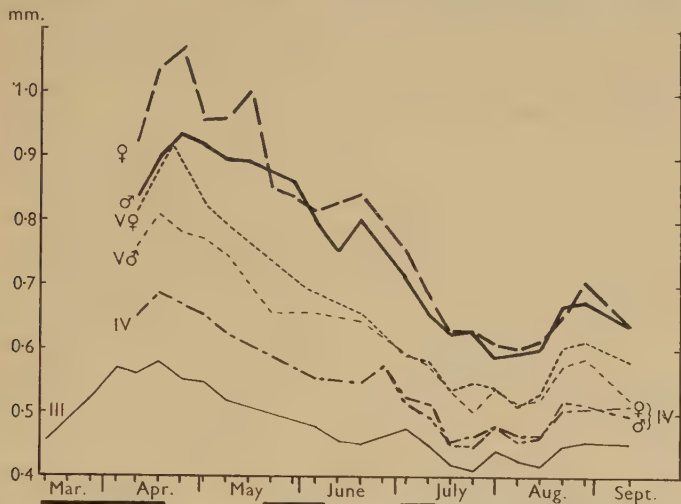


Fig. 24. *Temora longicornis*. Median size of copepodite Stages III-VI throughout the year. Lines as in Fig. 16.

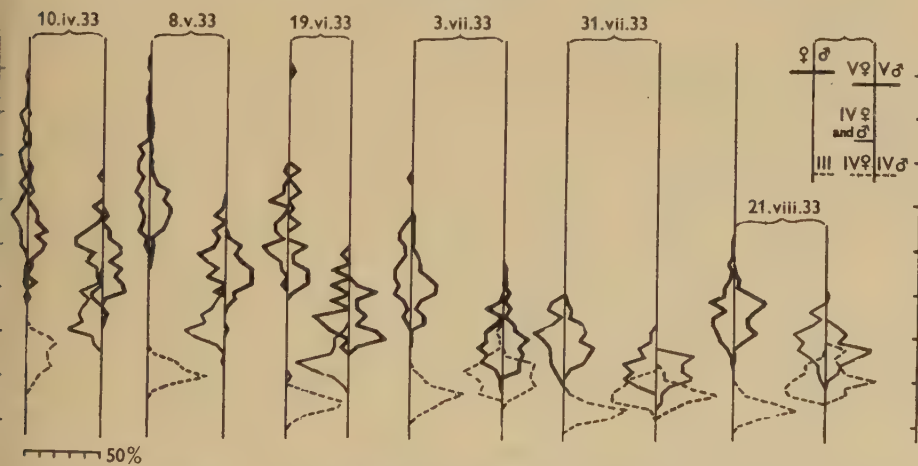


Fig. 25. *Temora longicornis*. Percentage size distribution of Stages III-VI on selected dates.

of one stage, apart from a few exceptional individuals, scarcely overlaps that of the next.

Oithona (Table XVI and Figs. 28, 29) varied less in size than the other copepods, although there was a gentle rise till the end of April and a subsequent decline. It resembles *Microcalanus* in its lack of a well-marked maximum in

spring. There was a slight rise again from 29 May to 19 June which coincided with a diatom increase and also with an increase in the number of eggs produced. After this the size decreased gradually, and by the beginning of August had reached that found in January, where it remained. From January

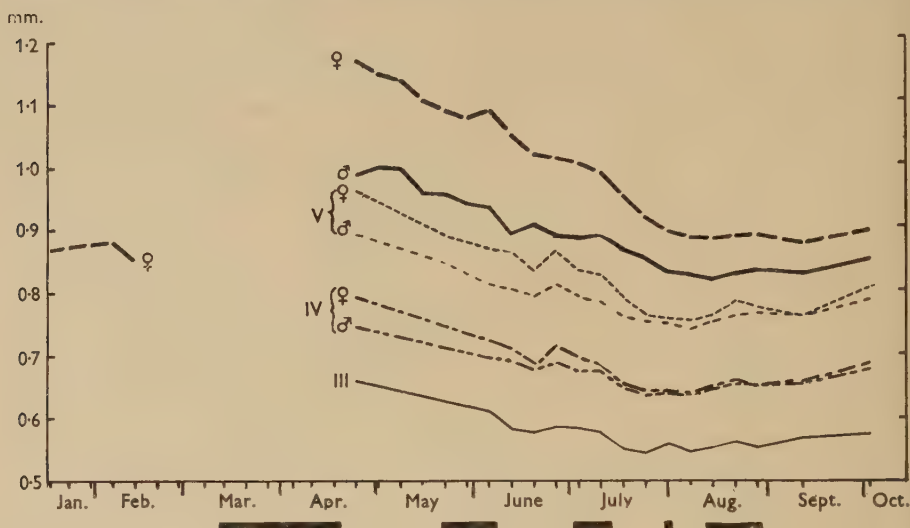


Fig. 26. *Acartia clausi*. Median size of copepodite Stages III-VI throughout the year. Lines as in Fig. 16.

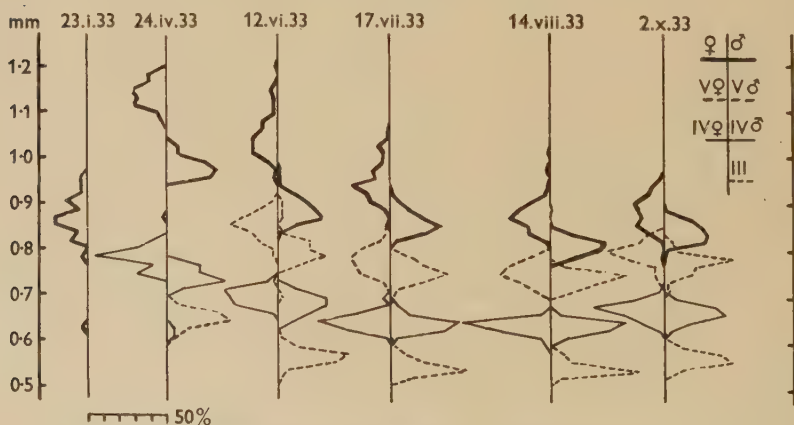


Fig. 27. *Acartia clausi*. Percentage size distribution of Stages III-VI on selected dates.

to mid-April the size range of Stage V overlapped almost completely those for both males and females (Fig. 29). For several weeks the median size of males was larger than that of females (Fig. 28) and for 2 weeks Stage V was larger also. If Fig. 29 is examined, however, it will be seen that this is because the

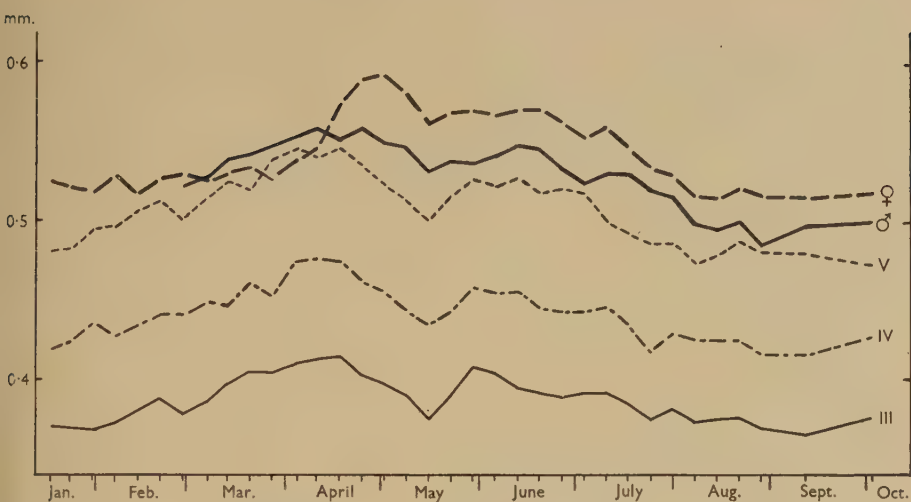


Fig. 28. *Oithona similis*. Median size of copepodite Stages III-VI throughout the year. Lines as in Fig. 16.

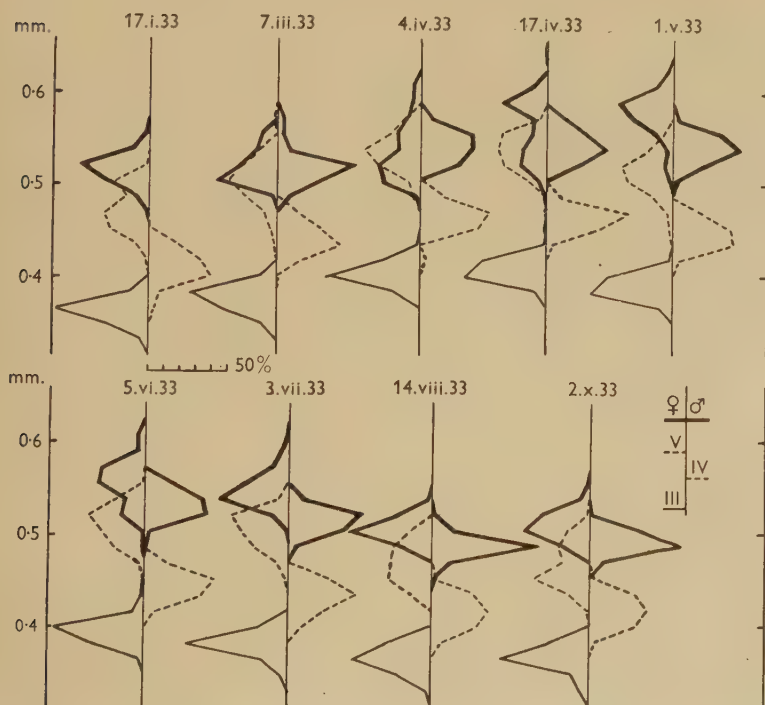


Fig. 29. *Oithona similis*. Percentage size distribution of Stages III-VI on selected dates.

Stage V of the spring brood had appeared. At this time the size-frequency curves for females show two modes, one belonging to the new large-sized brood, and one to the old small-sized brood (Table XVI). The female stock as a whole shifts from the old to the new mode during 27 March to 24 April, so that the fact that the median size of the Stage V is larger than that of the female merely means that the new-brood Stage V is larger than the old-brood females.

In every copepod species the maximum size was reached on the appearance of the spring brood in April. This brood hatched and grew up during that time of year when the sea was at its coldest. It was also a time of abundant diatoms, so that both low temperature and rich food supply may be held accountable.

In *Calanus* it was supposed (Marshall *et al.*, 1934) that the decrease in size during the summer was temporarily checked on the appearance of each new brood. This was certainly not true of the small copepods. In them the slight increases in size which occurred during the summer were hardly significant and bore no relation to broods. Even *Microcalanus*, which in its reproduction resembled *Calanus* closely, showed no comparable size changes. Only in the *Temora* females of the second brood on 15 May was there an increase in size, but this was based on the measurement of ten specimens only.

In East Greenland, where copepods have only one brood a year and the temperature change is marked only in the top 10 m., Ussing (1938) says that their size is influenced by two factors, the size at moult and the amount of food available. Temperature changes do not explain the size differences, for the largest copepods are found there in summer when the temperature is at its maximum. If one examines the diatom-rich periods along with the median-size curves of the Loch Striven copepods (Figs. 16, 18, 20, 22, 26, 28), it will be seen that there is little obvious correlation apart from the spring diatom increase. With a few exceptions the numerous diatom increases in the course of the summer are not marked by any significant changes in size. The August diatoms may be responsible for the increase in size of *Centropages* and *Temora* in late autumn, but if so, it is difficult to see why they did not have an effect on the other species too. *Pseudocalanus* and *Paracalanus* had stopped breeding by then, but in several of the others development seemed to have been still going on. The diatom-rich period from 29 May to 5 June may have been responsible for the slight increase in size of all stages of *Oithona* at that time; it certainly seems to have had an effect on egg production.

Adler & Jespersen (1920) carried out a long series of measurements of *Calanus*, *Pseudocalanus* and *Temora* on samples taken for several years from two lightships off the Danish coast, one in the North Sea and one in the Kattegat. In their *Pseudocalanus* measurements there was a very marked size maximum in mid-April every year and a more gradual decline, showing numerous irregularities, to a minimum in August. In the North Sea this

minimum size was retained all winter and there was no increase till the following March. In the Kattegat, however, in two of the three autumns the size increased sharply again in October and November and rose more or less steadily till April. It seems possible that breeding there continued later into the winter and that the lower temperatures then had an effect on the size of the developing copepods, but there is no obvious reason for a late brood. On the whole, however, the size changes agree very well with those found in Loch Striven except that in their samples the male is always about 0.1 mm. smaller than the female, and this difference is maintained throughout the year.

In *Temora* (adults only were measured) they found two maxima in the year, one in spring and the other in winter, usually December. This second maximum was sometimes even larger than the spring one, and perhaps indicated breeding during the winter. The measurement of the Loch Striven samples was not carried on far enough into the winter to see whether the size increase shown in the end of August continued. The actual sizes of the copepods were much the same in all three places, those from the North Sea being on an average rather larger than those from the Kattegat, and those from the Kattegat in turn rather larger than those from Loch Striven.

FOOD AND FEEDING

In examining the samples for measurement a note was kept of any copepods with food pellets in the gut. The copepods had been in preservative for up to 10 or 12 years, and the body was often opaque, making the gut difficult or impossible to see. No great reliance can be put therefore on the figures for the percentage feeding, and it seemed to have very little relation to the times of diatom increase. The greatest differences were found between one species of copepod and another. Thus *Temora* and *Centropages* always had a much larger percentage feeding than any of the other species, a fact which confirms observations made on living specimens (Lebour, 1922; Marshall, 1924). On the whole fewer males were seen with food than any of the other stages, and this is what might be expected from their shorter life and specialized function. In some copepods, e.g. *Euchaeta norvegica* (Sars, 1903; Nicholls, 1934), the male has much reduced mouthparts.

The results of some examinations of the gut contents of living copepods, taken from near the Marine Station, Millport, is shown in Table II. Most of these observations were made in autumn and winter, few in spring or summer. It will be noted that *Centropages* and *Temora* have again a larger proportion feeding than *Pseudocalanus* and *Acartia*.

As with *Calanus*, the food actually observed does not seem enough to meet the requirements, and the question remains whether or not the copepods depend largely on the minute naked flagellates about whose abundance and variations in the sea so little is known. Minute flagellates were counted in the

1933 centrifuged water samples (Marshall *et al.*, 1934, p. 824), but centrifuging is not a reliable method for these very small forms, and the figures given may bear little relation to their real abundance. It is perhaps not surprising, therefore, that no relation can be seen between their numbers and copepod size or breeding.

TABLE II

Species	No. examined	Empty or food indistinguishable	Diatoms	Radio- larians	Flagel- lates	Crustacea
<i>Pseudocalanus</i>	102	73	18	4	1	10
<i>Microcalanus</i>	16	15	1	0	0	0
<i>Centropages</i>	8	2	3	0	2	6
<i>Temora</i>	43	5	28	9	7	18
<i>Acartia</i>	88	59	18	3	1	9

Sixteen *Oithona* females were examined, but they contained only indistinguishable debris.

PARASITES

Pseudocalanus was the only copepod in which parasites were observed, and it seems to be less subject to them than *Calanus*. A trematode has occasionally been seen in its body cavity (although not in the Loch Striven samples), but the internal dinoflagellate parasites so common in *Calanus* (Jepps, 1937) are rare. Ten specimens were seen carrying *Ellobiopsis* and, as usual, most of these were on females (4 on Stage V female, 1 on Stage V male, and 5 on adult female). A *Microniscus* sp. was found on one female.

COMPARISON WITH OBSERVATIONS ELSEWHERE

Pseudocalanus. Among the pelagic copepods, *Pseudocalanus minutus*, because of its large numbers, is perhaps the most important species after *Calanus*, and its breeding and size variations have been studied in numerous places in the North Atlantic. The general course of its growth and development there is remarkably uniform. In Loch Striven, off the Norwegian coast (Oslo Fjord, Wiborg, 1940; Herdla and Hjelte Fjords, Runnström, 1932; off Möre, Ruud, 1929), and in the seas between Norway and Iceland (Störmer, 1929), reproduction begins in early spring, usually at the time of the phytoplankton increase, and goes on throughout the summer. The maximum numbers occur, not with the first brood, but during the summer, and by July or August the stock is mainly in the late copepodite stages and will pass the winter thus. In Nordåsvatn, however, Stage III is the most abundant stage from August to December (Wiborg, 1944). In the most southerly area investigated, the Gulf of Maine, much the same holds good (Fish, 1936*b*); reproduction begins with the spring increase and there are three or four broods during the summer and autumn, of which the second is the largest, but the copepod almost disappears from inshore waters from July to October. Fish supposes that rising temperature is the cause of this and that they move into deeper water offshore.

In the most northerly part of the area, East Greenland, conditions are rather different (Ussing, 1938). Most of the stock spends the winter in deep water (below 50 m.) and rises above this only from June to August. Reproduction begins soon after, but in the cold water there development is slow and there is only one brood a year, although a few individuals may possibly grow fast enough to reproduce in the same summer that they are hatched. Early copepodite stages are found throughout the winter, and even Stage II does not entirely disappear till March of the year following that in which it is hatched. The temperature below 50 m. differs little from that above except near the surface during the summer, and Ussing ascribes the seasonal vertical migrations to the influence of light.

Pseudocalanus is found at all depths, but as a rule is more abundant near the surface, i.e. above 50 m., and even above 20 m. (Ruud, 1929). According to Runnström (1932) it avoids the layers above 10 m., but this was not so in Loch Striven. Ruud records that in 1927 at two Stations it was more numerous below than above 50 m. in May, June and July. Where vertical hauls have been taken in sections the division has commonly been made much deeper than 10 m., so that the seasonal migration above and below 10 m. found in Loch Striven cannot be confirmed from elsewhere. In Nordåsvatn, a land-locked fjord near Bergen, *Pseudocalanus* was often found above 15 m., and there were considerable alterations in vertical distribution from time to time (Wiborg, 1944). Hydrographical conditions were, however, so different (well-marked layering, and lack of oxygen in deep water) that the two areas can hardly be compared.

In the Barents Sea (Bogorov, 1932) the depth distribution was peculiar in that there were maxima at 10–25 and 100–160 m., with an intervening minimum. The upper maximum is composed of Stages I–V, the lower of Stages III–VI.

Paracalanus. In Norwegian waters (Runnström, 1932; Wiborg, 1940) *Paracalanus* is scarce throughout the winter and has a maximum in late summer as in Loch Striven.

Microcalanus. This copepod, owing to its small size, will slip through the meshes of most nets and has not been taken into account in most plankton hauls. There are, however, some data on its occurrence off the Norwegian coast (Ruud, 1929; Runnström, 1932; Wiborg, 1940), and from the *Michael Sars* expedition (Störmer, 1929). It is generally agreed to be a deep-water form living mainly below 50 m. Runnström states that in autumn and winter (in the Herdla and Hjelte Fjords) it is numerous also from 10 to 50 m., and that from May to August it is found mainly below 100 m. Störmer mentions the possibility that it may make diurnal vertical migrations. The dates of spawning, which they judged mainly from the presence of males or of females carrying spermatophores, agree well with those in Loch Striven, March (off Möre), or February to April (Oslo Fjord), May (Herdla and Hjelte Fjords), May to June

(off Möre), or June (Oslo Fjord), October to November (Oslo Fjord). Wiborg remarks on the periodicity of the spawning, and his late autumn date is perhaps an indication that spawning can go on during the winter. There was in the Loch Striven samples, however, no clear development from the nauplii even as early as August.

In the fjords of East Greenland (Ussing, 1938) *Microcalanus* was found above 50 m. only in winter (November to May). It spawned in the early months of the year (January to March), but this was probably not the main spawning time. Owing to its withdrawal into deep water during the summer, its complete life history there could not be ascertained.

Centropages hamatus. This is a coastal form living near the surface and there are few observations on it in the literature. Wiborg (1940), working in the Oslo Fjord, says that the chief spawning is in March or April, but that there is some also in summer. The maximum numbers are in June and July when adults and copepodites predominate. On the whole this agrees fairly well with Loch Striven. Otten (1913) says that in Kiel Bay its numbers increase gradually till June, decrease, and then increase again in September. As already mentioned (p. 59) he found a large number of nauplii but no copepodites in the end of September and even in November.

In the zooplankton of the Gulf of Maine (Fish & Johnson, 1937) *C. hamatus* was not present but *C. typicus* occurred, and they mention the possibility of its having a 'winter egg' since the species is sparse or absent most of the year.

Temora. Like *Centropages*, *Temora* is a neritic form, living near the surface, abundant as a rule only in summer. In the Oslo Fjord (Wiborg, 1940) it was scarce during the winter and numerous from April till July. The maximum numbers in the outer fjord were found in April and July, and the main spawning was (as in Loch Striven) in April. Nauplii were found all the year round, and adults were more numerous from June to October. This was not so in Loch Striven, nor was the proportion of adults higher than in the other species. Males outnumber females in the Oslo Fjord but not, according to Otten (1913) in Kiel Bay (see Table I). There reproduction probably went on late into the winter, since maxima of copepodites were found in June, September and also December.

Acartia. In the Oslo Fjord (Wiborg, 1940), as in Loch Striven, *Acartia* had a late summer maximum in numbers and decreased very much from December to June. In other areas, however, such as the Herdla and Hjelte Fjords (Runnström, 1932) and off Möre (Ruud, 1929), there were two maxima, the first in April to May or May to June and the second in July or August to November. Off Möre there were several broods in the year beginning in March to April. *Acartia* has usually been found between 0 and 100 m., but in autumn was found also down to 200 m.

On the east coast of America this species occurs as an inshore form. South of Cape Cod (Fish & Johnson, 1937) it forms an important part of the neritic

community in winter, but to the north it has its maximum in late summer and usually spawns then. It is occasionally found to spawn in early spring there also, but this may be an extension of the winter breeding centred to the south of Cape Cod.

Oithona similis. This is a very widely distributed species, and its seasonal variation in numbers has been studied in the Gulf of Maine (Fish, 1936c) as well as in the North Atlantic and on the Norwegian coast.

In Norwegian waters the species is found down to 400 m., although it is commonest near the surface. It occurs all the year round and has two maxima in numbers, one in March to May, the other July to August, the date varying from year to year.

Otten (1913), working in Kiel Bay, finds rather different conditions, for he states that maximum numbers occur in April and in October with a minimum in August. This indicates a condition very different from Loch Striven where the maximum comes in August.

Fish (1936c) finds that in the Gulf of Maine, as in Loch Striven, eggs and nauplii make up a large proportion of the total catch throughout the year, indicating a heavy mortality in these stages. He suggests, however, that development takes as long as 2 months in winter and 6 weeks in summer, which seems decidedly too long for the Loch Striven *Oithona*. Breeding in the Gulf of Maine as in Loch Striven begins in March, and three or four broods are produced from then till September. The maximum number occurs in August.

DISCUSSION

The importance of a copepod in the ecology of the plankton cannot be judged from its numbers alone; its size must also be taken into account. Very little is known about the weights of the small copepods. Bogorov and Preobrajenskaya (1934) have published a few data for *Pseudocalanus elongatus* (Stages V and VI), *Centropages hamatus* (Stage VI) and *Acartia longiremis* (Stage VI), giving the average dry weights as 0.07–0.09, 0.11 and 0.012 mg. respectively. Lohmann (1908) has given calculated volumes in cubic microns for most of the common species, but his relative values (which are rough averages from nauplius as well as copepodite stages) do not agree very well with the Loch Striven sizes. His volumes for the different species in cubic millimetres are as follows: *Temora*, 0.026; *Centropages hamatus*, 0.025; *Pseudocalanus*, 0.0235; *Acartia*, 0.014; *Paracalanus parvus*, 0.006; *Oithona similis*, 0.003. In this series *Temora* seems too large and *Acartia* too small; *Microcalanus* would presumably be slightly larger than *Oithona*. He does not give *Calanus* either, and it is probably at least ten times the volume of *Pseudocalanus*. Fig. 30 shows the numbers of the seven species of copepod in Loch Striven throughout the year, all drawn on the same scale. Taking Lohmann's values for volume it is found that (apart from *Calanus*) *Pseudocalanus*, because of its size and abundance, is by

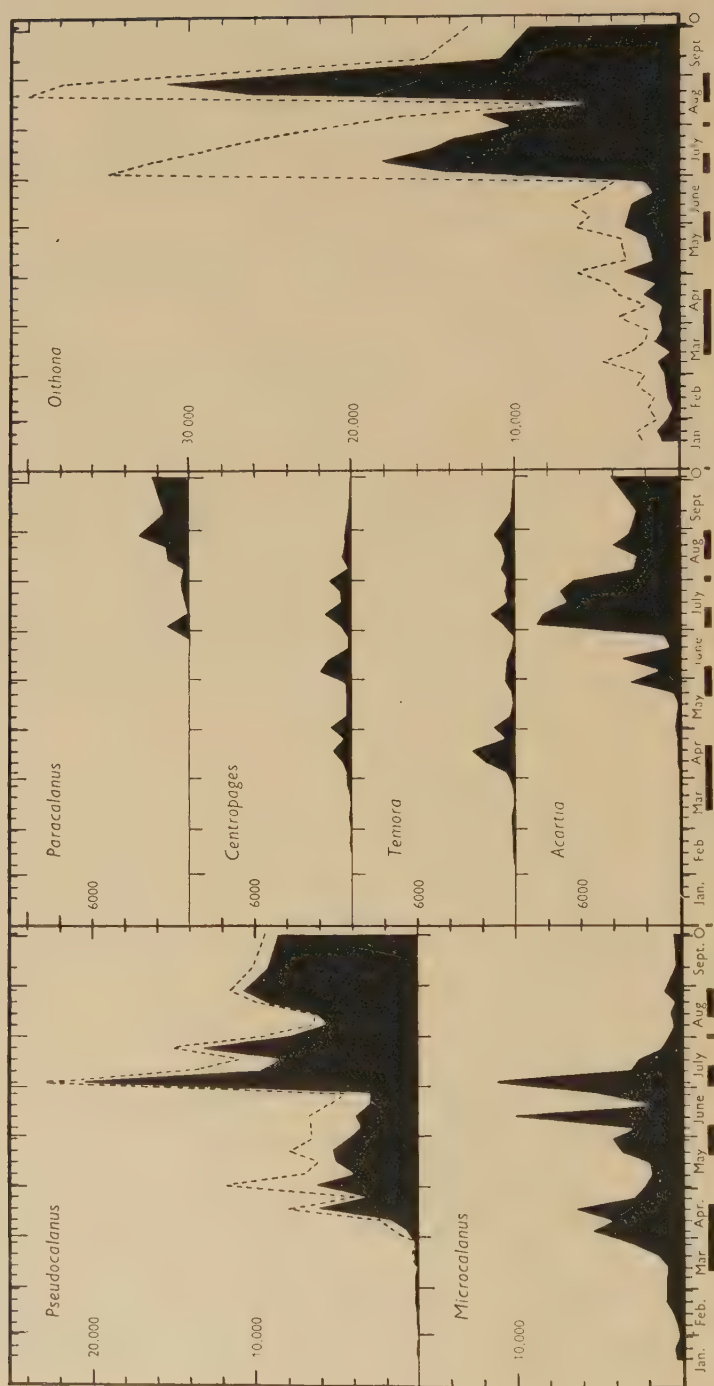


Fig. 30. Total numbers of the seven copepods throughout the year all shown on the same scale. Solid black, nauplii and copepodites, dotted line (*Pseudocalanus* and *Oithona*), total including eggs.

far the most important, *Acartia* (even at Lohmann's low assessment) comes next, and *Oithona*, because of its high numbers, third. *Microcalanus*, *Temora* and *Centropages* are all much the same and considerably less than *Oithona*. This gives a rough idea of the amount of animal food each copepod species can provide. *Paracalanus* is omitted, since it did not become common till July and may have been more important after observations stopped in October. The different stages and species of copepod are, however, eaten by different sizes of fish, the smallest stages providing food for the larvae and the largest for post-larval or even adult fish. Some of this food is available all the year round, but it is most abundant from April on throughout the summer when most young fish are growing.

The life histories of all the copepods so far examined resemble one another in their general features and differ only in detail. Each shows a succession of broods throughout the summer, sometimes distinct but more often running into one another. The dates on which breeding begins and stops vary from year to year and from place to place. The usual number of broods is three or four, but in the cold waters of the far north this may be reduced to one. Since work in Loch Striven stopped in October it is not possible to say for every species whether breeding continued after this date or not. In *Calanus*, *Pseudocalanus* and *Paracalanus* it certainly did not, for by that time a large stock (40–80 % of the total catch of each) of Stages IV or V had been built up, and further development had obviously stopped. In the other copepods a much larger proportion of nauplii was present in October (about 75 % in *Microcalanus*, *Centropages* and *Temora*), and although breeding did not seem to be going on it was still a possibility. In *Acartia* and *Oithona* the percentage of nauplii in October was about 40 %, much lower than was found in January to March. Here, too, further breeding was still possible. The stage in which the winter is passed may therefore vary in different species of copepod, and further work is needed to elucidate this.

The sequence of events described, although true for 1933, may not be followed every year. It is known from unpublished observations in Loch Striven and at Millport that, for instance, *Microcalanus* is not always one of the common copepods, and that the order of appearance and relative abundance of the different species is not always the same. It would therefore be very interesting to have detailed studies of the copepods, not only from different areas, but from the same area in different years.

The vertical distribution of the copepods in Loch Striven was rather different from that described elsewhere, mainly perhaps because the loch is, comparatively speaking, shallow, and the great depths at which they are sometimes found do not occur there. In Loch Striven all but *Microcalanus* followed the same pattern; they were all near the surface till July, and then the older stages were mainly in deeper water for at least a few weeks and in some species a few months.

The seasonal size variations, too, resembled each other closely in all species examined and agreed with what has been found elsewhere. The different species do not all grow at the same rate. Fig. 31 shows the median size of all the copepodite stages of all the copepods on 3 July (see also Table XVII), a date when they were numerous enough to measure, and Fig. 32 shows the maximum and minimum sizes reached during the year by each stage. It

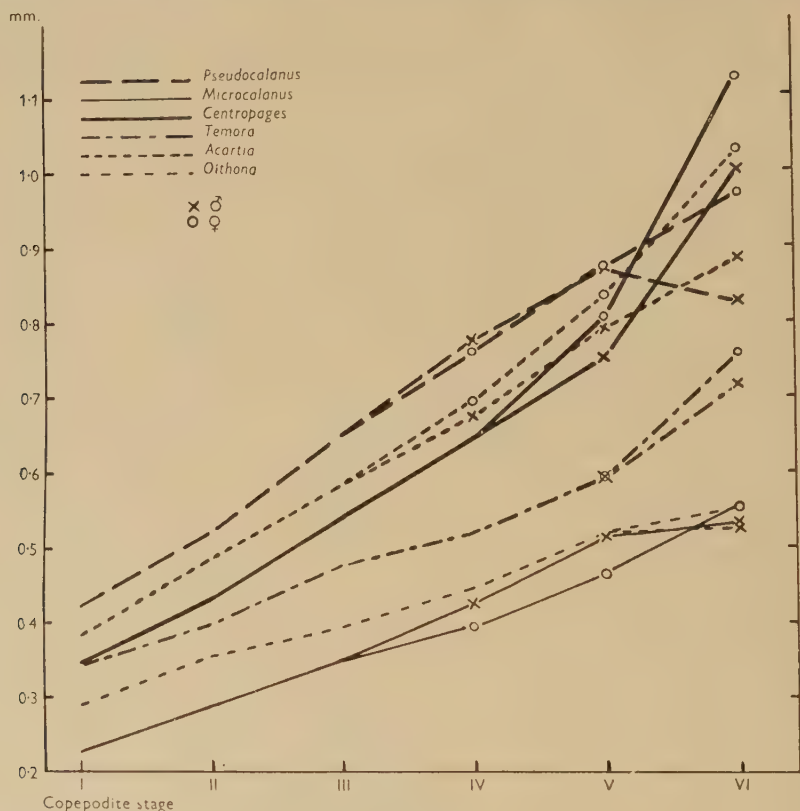


Fig. 31. Median size of copepodite Stages I–VI of six copepod species on 3 July.

can be seen from Figs. 31 and 32 that whereas *Oithona* doubles its length from Stage I to the largest Stage VI, *Pseudocalanus*, *Microcalanus*, *Temora* and *Acartia* about treble it and *Centropages* quadruples it. From Stage I to Stage V (Fig. 31) *Pseudocalanus* and *Acartia* are about the same size as *Centropages*, but in the adult, *Centropages* is the largest.

The points for the median lengths of the stages in each copepod lie on a more or less straight line up to Stage V, but beyond this the different species vary. In *Centropages* there is a marked, and in *Temora* and *Acartia* a slight, rise in the curve from Stages V to VI, in each case greater in the female than

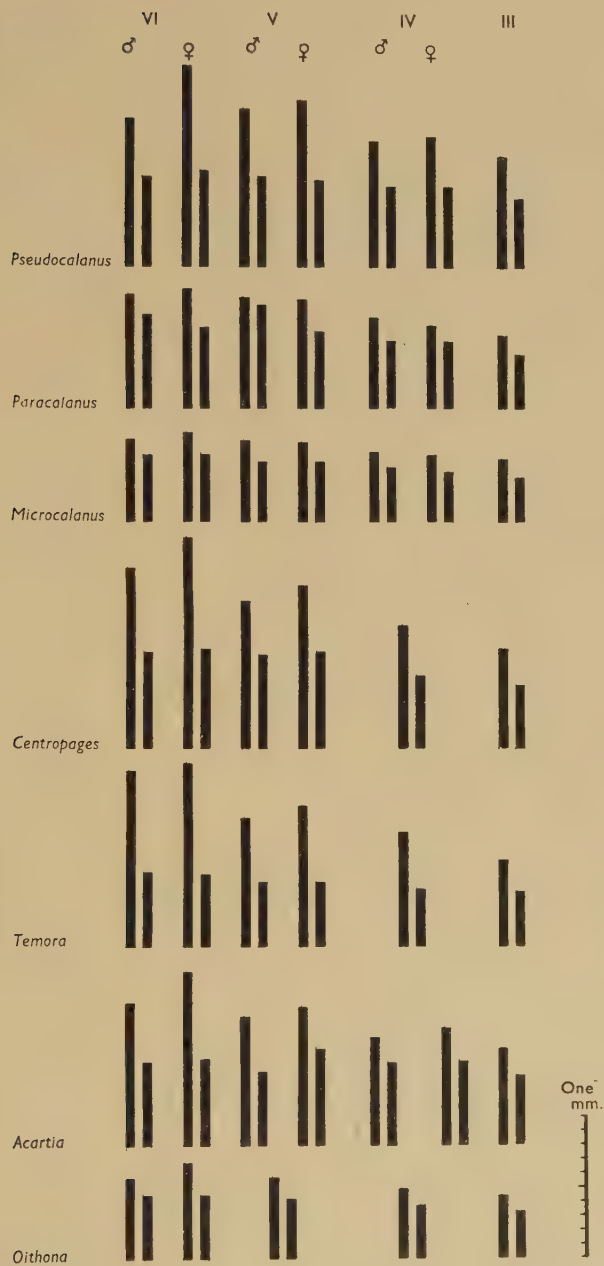


Fig. 32. Maximum and minimum sizes of copepodite Stages III-VI in seven species.

in the male. In *Pseudocalanus* and *Microcalanus* the female continues on the same straight line as before, whereas the male curve flattens off, the male increasing only slightly in size in *Microcalanus* and actually decreasing in *Pseudocalanus*. In *Oithona* the curve flattens off in both sexes, the male increasing rather less than the female.

An interesting but difficult point to settle is the relation between diatom increases, the production of broods and the size of the copepods. In their study of the sizes of several species of copepod in the North Sea and Kattegat, Adler & Jespersen (1920) came to the conclusion that temperature was the most important factor. Ussing (1938), on the other hand, working off East Greenland, thought that food in the form of phytoplankton was much more important.

The diatom most common in Loch Striven was *Skeletonema costatum*, a species with cells small enough to be eaten by all the copepods at least in their later stages. This species formed practically all the spring increase and was predominant up till 24 July. After that *Leptocylindrus* sp. and *Chaetoceros* spp. were more important. Table II (p. 84) indicates that *Centropages* and *Temora* are less dependent on diatoms than the rest because they are voracious feeders and eat Crustacea and other organisms as well as diatoms, and that, since *Microcalanus* and *Oithona* are rarely found with recognizable remains in the gut, they may feed mainly on smaller organisms such as minute flagellates. Much is still unknown about the nature of the food and the food requirements of the copepods, and until more has been found out about the relation of these to the nanoplankton any conclusions must be only tentative.

The connexion of the spring brood with the spring diatom increase has already been mentioned. This early brood also attained the largest size in all but one species. In *Microcalanus* the largest copepods occurred during April and may have consisted mainly of the brood produced before the spring diatoms increased. This suggests a temperature effect rather than a rich food supply, or perhaps that this species does not depend on diatoms for food (see above). The spring brood of all the copepods grew up when the sea was at its coldest, and it may be suggested that temperature is important, not only for *Pseudocalanus*, but for all copepods with a similar size curve. Indeed, the correlation coefficient between the size of *Pseudocalanus* females and the temperature of a month before (to allow for growth from egg to adult), both sets of figures being grouped as monthly averages, is significant (0.88), although the observations available (7 pairs) are few.

When we examine Figs. 1-14 it can be seen that there are both diatom increases without peaks in nauplii, and peaks in nauplii when diatoms are poor. From 22 May to 5 June diatoms were rich, yet although there were increases both in the proportion and in the actual number of nauplii (*Pseudocalanus* was an exception), no brood grew up. The diatom increase on 3 to 10 July, on the other hand, was accompanied in almost every copepod by an increase in nauplii

from which a brood grew up. The very short-lived diatom increase on 31 July (164 cells/ml. at the surface only) had no effect except a possible increase of nauplii in *Centropages*. The larger and more prolonged increase from 14 to 18 August was again accompanied by an increase in nauplii in every copepod, but since breeding at that time was more or less continuous it is doubtful whether an increase in the number of older stages resulted.

On the other hand, on 1 May, when diatoms were poor, there was a peak of nauplii followed by a brood in *Centropages*, *Temora* and possibly *Oithona*. These are, however, three of the copepods which may be less dependent on diatoms for food than are the others (Table II, p. 84).

On the whole, then, it does seem that the presence of diatoms increases the production of eggs and nauplii and helps the development of the later stages.

SUMMARY

The seven species of small copepod common in Loch Striven have been studied from vertical tow-net hauls taken there throughout the year 1933. These copepods were *Pseudocalanus minutus*, *Paracalanus parvus*, *Microcalanus pygmaeus*, *Centropages hamatus*, *Temora longicornis*, *Acartia clausi* and *Oithona similis*.

In general, the copepods began to reproduce about the time of the spring diatom increase in March or April, and produced a succession of broods throughout the summer; apart from the first these broods were not as a rule so clearly marked as in *Calanus*. *Microcalanus* begins to breed before the spring increase and has clearly marked broods like *Calanus*.

The numbers of males and females were about equal until the adult stage, when the proportions varied greatly between one species and another.

The number of eggs laid per female was counted in *Pseudocalanus* and *Oithona* and it varied throughout the year. The number is closely correlated with the size of the female and may bear some relation to the amount of phytoplankton present.

With the exception of *Microcalanus* all the copepods showed a seasonal vertical migration. From April till the beginning of July they were found mainly above 10 m. and in July and August mainly below. The migration was more marked in some species than in others and, as in *Calanus*, the younger stages showed it less than the older. *Microcalanus* stayed below 10 m. almost entirely from April to August.

The size of copepodite Stages III–VI was measured throughout the year. In most species there was a well-marked maximum in spring and a gradual decrease till the autumn. The relative size of male and female in copepodite Stages IV–VI is different in different species.

Observations in Loch Striven are compared with those made on the same copepods elsewhere.

The relationship between reproduction, size and phytoplankton is discussed.

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TABLE III. PSEUDOCALANUS MINUTUS. NUMBER PER HAUL

TABLE III. PSEUDOCALANUS MINUTUS. NUMBER PER HAUL

(For meaning of symbols see end of table)

[illegible]

12. vi	(B-10	24	45	52	165	87	37	25	645	1052	20.4	1080	3766
	(B-10	79	177	222	131	187	204	176	1510	1888		2686	
19. vi	(B-10	8	16	24	90	21	8	8	214	53	19.6	391	1432
	(B-10	50	84	85	123	148	85	24	442	666		1041	
19. vi	U.H. B-o	1	346	194	302	158	184	48	1768	2681	19.8	3166	
19. vi	U.H. B-o	2	276	202	388	216	154	47	1648	2793	19.9	3047	
19. vi	U.H. B-o	3	280	152	424	248	138	41	1328	2466	19.9	2723	
26. vi	(B-10	1	24	23	114	35	4	10	222	256	17.4	433	2496
	(B-10	..	1	..	1	..	..	21	2040	22		2063	
26. vi	U.H. B-o	1	310	113	374	135	20	77	1440	2646	19.1	2491	
26. vi	U.H. B-o	2	216	115	565	175	32	107	2180	1863	19.8	3418	
26. vi	U.H. B-o	3	138	85	466	136	40	104	1850	1198	18.6	2840	
26. vi	U.H. B-o	4	144	105	590	149	19	127	1610	1263	18.6	2757	
3. vii	(B-10	68	358	402	4050	740	264	162	492	2052	15.6	6536	15,370
	(B-10	..	3	2	19	8	18	184	8600	82		8834	
3. vii	U.H. B-o	94	635	610	5080	1140	810	1310	10,680	2408	15.3	20,359	
10. vii	(B-10	92	450	990	2180	1050	605	328	610	2656	14.1	6305	6580
	(B-10	..	2	5	8	5	3	12	240	..	..	275	
10. vii	U.H. B-o	104	563	619	2498	1136	906	900	3116	3563	14.0	8248	9842
17. vii	(B-10	205	527	712	3595	499	437	793	1480	2589	15.4	131	8379
	(B-10	..	4	1	16	8	5	6	91	6	..	8713	
24. vii	(B-10	107	374	855	4720	1260	490	82	825	1819	11.4	289	9002
	(B-10	..	1	1	20	6	5	5	251	..	..	13,103	
24. vii	U.H. B-o	200	575	1420	6900	1770	750	268	1220	1898	11.6	5437	5755
31. vii	(B-10	61	242	575	2460	795	510	204	590	1347	9.8	318	7904
	(B-10	1	1	3	12	7	24	10	260	..	..	3718	5494
31. vii	U.H. B-o	107	510	990	3760	785	448	284	1020	1474	10.9	1776	3467
7. viii	(B-10	30	224	250	2900	185	59	13	57	992	10.1	1956	6237
	(B-10	1	..	3	31	12	42	87	1600	..	..	1511	7275
14. viii	(B-10	4	11	62	1800	38	9	3	29	6	6.0	5592	9262
	(B-10	1	1	1	27	..	10	31	1440	..	..	1883	10,737
14. viii	U.H. B-o	27	67	232	4310	212	234	165	990	88	9.2	9247	8472
21. viii	(B-10	46	121	312	3030	675	740	324	344	415	9.8		
	(B-10	..	..	12	53	98	200	310	1010	..	..		
21. viii	U.H. B-o	37	155	385	3760	1050	1370	795	1710	605	10.5		
28. viii	U.H. B-o	102	520	735	5090	1160	1000	550	1580	745	9.8		
11. ix	(B-o	80	505	495	5600	910	126	181	1350	922	8.0		
2. x	U.H. B-o	44	410	730	4590	414	220	174	1890	972	10.0		

U.H. Undivided hauls.

* Excluding eggs.

+ One undivided haul.

‡ Average of two undivided hauls.

|| Average of five undivided hauls.

§ Average of four undivided hauls.

TABLE IV. *PARACALANUS PARVUS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
3. vii	B-o	..	..	..	..	..	..	..	1362	1362
10. vii	{B-10 10-o	..	..	..	I	..	..	..	90*	94
10. vii	U.H. B-o	..	..	..	..	..	..	3		
		Not counted								
17. vii	{B-10 10-o	..	..	I	2	6	2	I	169*	206
		..	..	I	I	3	6	14		
24. vii	{B-10 10-o	..	5	I	3	..	..	7	348*	423
		..	2	I	I	9	7	38		
24. vii	U.H. B-o	I	18	20	5	15	10	3	245*	480
31. vii	{B-10 10-o	2	8	14	26	20	5	..		
		I	I	7	9	14	23	79	159*	289
31. vii	U.H. B-o	2	13	38	72	57	28	58		
7. viii	{B-10 10-o	..	9	6	..	..	I	I	679*	892
		I	I	9	15	44	24	19		
14. viii	{B-10 10-o	..	2	2	..	..	..	8	148	296
		..	I	2	5	22	70	168		
14. viii	U.H. B-o	2	21	15	3	8	29	64	525	979
21. viii	{B-10 10-o	2	11	43	53	28	7	4	650	1416
		..	5	20	118	181	92	38	1750	3066
21. viii	U.H. B-o	6	40	120	205	205	85	105	450	1632
28. viii	‡B-o	40	240	196	170	154	212	304	405	2252
11. ix	§B-o	18	100	192	308	234	202	128		
2. x	‡B-o	11	72	315	575	390	272	212		

* The nauplii were picked out after the hauls had been mixed and the figure is therefore an average only.

† One undivided haul.

‡ Average of two undivided hauls.

§ Average of five undivided hauls.

TABLE V. *MICROCALANUS PYGMAEUS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
7. i	§B-o	I	7	7	16	16	22	16	180	265
23. iii	§B-o	4	14	35	25	7	9	23	322	439
30. iii	§B-o	I	5	8	7	5	21	40	136	223
6. ii	§B-o	6	41	54	17	14	17	44	153	346
13. ii	§B-o	8	30	37	35	71	85	61	209	536
20. ii	§B-o	23	40	70	118	129	125	96	324	925
27. ii	§B-o	3	45	82	58	67	66	38	495	854
7. iii	§B-o	50	139	109	43	11	10	6	488	856
13. iii	§B-o	59	91	116	42	10	4	25	441	788
20. iii	‡B-o	78	135	94	7	6	24	30	1058	1432
27. iii	B-10	9	8	6	I	4	7	94	1894	2023
	10-o	I	24	5	11	63	41	125	572	842
4. iv	B-10	45	73	22	23	28	60	210	3621	4082
	10-o	..	4	18	34	111	140	152	906	1365
10. iv	B-10	33	51	31	32	59	85	147	3451	3889
	10-o	..	3	I	4	3	I	I	159	172
17. iv	B-10	21	83	73	56	76	91	101	5712	6213
	10-o	I	3	4	3	7	6	9	159	192

TABLE V (cont.)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
24. iv	{B-10	13	81	33	56	80	111	150	292	816}
	{10-0	..	I	I	2	5	2	2	6	19}
24. iv	‡U.H. B-0	85	517	308	338	304	379	366	544	2841
I. v	{B-10	41	292	384	294	302	183	95	36	2227}
	{10-0	..	..	I	..	I	..	..	4	6}
8. v	{B-10	16	105	104	47	19	8	9	876	1184}
	{10-0	..	2	I	..	I	..	..	I	5}
8. v	‡U.H. B-0	48	685	545	193	72	18	22	176	1759
15. v	‡B-0	186	305	410	152	32	12	24	772	1893
22. v	{B-10	47	238	149	19	5	6	31	3933	4428}
	{10-0	..	5	2	..	I	I	I	26	36}
22. v	‡U.H. B-0	106	505	336	29	26	35	70	2538	3645
29. v	{B-10	53	264	57	15	5	25	102	3523	4044}
	{10-0	I	7	..	..	3	I	3	90	105}
5. vi	{B-10	18	112	10	12	13	34	35	2920	3154}
	{10-0	..	4	..	..	I	I	2	81	89}
5. vi	‡U.H. B-0	43	464	26	16	29	46	89	1957	2670
12. vi	{B-10	6	585	34	35	64	69	79	8870	9742}
	{10-0	..	8	2	I	2	2	3	386	404}
19. vi	{B-10	I	105	10	14	4	5	11	1080	1230}
	{10-0	..	..	..	..	..	..	..	179	179}
19. vi	*U.H. B-0	..	240	22	26	21	20	18	1600	1947
19. vi	*U.H. B-0	3	344	35	31	8	12	19	1064	1516
19. vi	*U.H. B-0	3	158	20	15	13	7	11	186	1043
26. vi	{B-10	7	132	14	16	23	22	59	7240	7513}
	{10-0	..	..	..	..	..	..	..	74	74}
26. vi	*U.H. B-0	15	520	91	78	26	25	67	1750	2572
26. vi	*U.H. B-0	14	358	81	56	43	35	95	4740	5422
26. vi	*U.H. B-0	15	384	79	55	33	21	92	4950	5629
26. vi	*U.H. B-0	16	334	76	56	25	25	77	5670	6279
3. vii	{B-10	39	1060	224	83	71	82	69	4265	5893}
	{10-0	..	2	..	..	..	..	..	40	42}
3. vii	‡U.H. B-0	90	2280	386	190	130	258	352	7402	11,088
10. vii	{B-10	45	690	144	122	128	80	37	753	1999}
	{10-0	..	..	..	I	..	..	I	16	18}
10. vii	‡U.H. B-0	46	968	225	151	180	165	106	1122	2963
17. vii	{B-10	39	1120	190	122	62	39	15	937	2524}
	{10-0	I	I	I	..	I	..	..	18	22}
24. vii	{B-10	12	625	141	37	12	11	11	553	1402}
	{10-0	..	..	..	I	..	..	..	86	87}
24. vii	‡U.H. B-0	30	525	183	105	28	15	13	345	1244
31. vii	{B-10	13	268	86	32	18	12	5	199	633}
	{10-0	..	..	..	..	..	..	..	138	138}
31. vii	‡U.H. B-0	9	262	90	28	21	9	16	256	691
7. viii	{B-10	3	93	34	12	10	6	I	208	367}
	{10-0	..	..	2	..	..	..	..	65	67}
14. viii	{B-10	2	31	9	I	..	..	..	199	242}
	{10-0	..	..	..	..	..	..	..	382	382}
14. viii	‡U.H. B-0	7	75	22	6	2	2	2	458	574
21. viii	{B-10	I	41	4	..	2	..	..	256	304}
	{10-0	..	..	..	..	..	..	..	35	35}
21. viii	‡U.H. B-0	I	33	4	..	2	I	I	260	302
28. viii	‡B-0	3	76	16	16	2	3	3	890	1009
I. ix	§B-0	..	30	5	2	I	3	2	240	283
2. x	*B-0	4	40	12	9	3	15	8	310	401

* One undivided haul.

‡ Average of four undivided hauls.

† Average of two undivided hauls.

§ Average of five undivided hauls.

TABLE VI. *CENTROPAGES HAMATUS*. NUMBER PER HAUL
(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
17. i	‡B-o	..	..	..	..	..	..	..	15	15
23. i	‡B-o	..	..	..	..	..	..	+	17	17
30. i	‡B-o	..	..	+	..	..	..	..	8	8
6. ii	‡B-o	..	..	..	..	..	..	..	10	10
13. ii	‡B-o	..	..	..	..	..	..	..	32	32
20. ii	‡B-o	..	..	..	..	..	..	..	132	132
27. ii	‡B-o	..	..	..	..	..	..	+	39	39
7. iii	‡B-o	+	..	..	..	+	I	+	224	225
13. iii	‡B-o	..	..	..	..	..	..	+	87	87
20. iii	‡B-o	+	+	..	..	I	I	3	82	88
27. iii	B-10	..	..	I	..	2	I	4	36	44 } 265
	10-o	4	..	I	2	15	23	31	145	
	B-10	I	I	2	I	..	I	2	9	
4. iv	10-o	3	5	48	21	20	52	29	61	239 } 256
	B-10	I	I	I	..	..	I	..	15	
10. iv	10-o	31	21	22	32	33	33	24	276	472 } 491
	B-10	I	..	..	..	2	3	I	22	
17. iv	10-o	27	15	35	26	35	57	143	765	1103 } 1132
	B-10	2	..	..	I	I	I	..	45	
	10-o	21	15	20	52	79	51	18	435	
24. iv	U.H. B-o	13	33	13	33	18	18	10	388	691 } 741
	B-10	35	17	16	14	I	4	..	188	
I. v	10-o	19	19	35	15	9	24	37	905	1062 } 1337
	B-10	..	..	..	I	..	I	..	14	
8. v	10-o	12	3	15	18	31	54	119	1010	1262 } 1278
	U.H. B-o	22	8	15	10	9	17	39	201	
15. v	‡B-o	17	10	11	34	52	25	8	113	15 } 270
	B-10	I	..	I	..	I	..	..	12	
22. v	10-o	11	5	33	26	6	9	19	272	381 } 396
	U.H. B-o	20	6	47	23	9	9	19	160	
22. v	B-10	..	..	..	..	..	..	..	23	23 } 293
	10-o	..	2	2	3	14	26	60	258	
29. v	B-10	..	..	..	..	..	..	..	302	302 } 388
	10-o	..	..	..	3	6	20	27	5240	
5. vi	U.H. B-o	4	5	8	14	17	8	9	1824	119 } 1889
	B-10	3	..	..	..	I	2	I	112	
12. vi	10-o	33	10	11	6	10	20	59	1140	1289 } 1408
	B-10	4	I	I	..	I	..	..	13	
19. vi	10-o	12	3	3	I	I	I	2	228	251 } 271
	*B-o	28	11	2	I	I	I	2	192	
19. vi	*B-o	35	6	5	3	5	6	3	160	26 } 238
	*B-o	46	19	3	6	3	4	4	106	
26. vi	B-10	..	..	..	..	..	2	..	24	26 } 191
	10-o	..	..	..	..	..	I	16	262	
26. vi	*B-o	20	2	4	3	I	7	12	80	279 } 305
	*B-o	4	..	5	2	7	8	22	100	
26. vi	*B-o	2	..	..	I	4	9	16	123	26 } 129
	*B-o	5	..	5	2	9	13	15	128	
26. vi	B-10	4	2	14	28	8	I	..	6	63 } 177
	10-o	..	..	4	8	29	45	56	214	
3. vii	U.H. B-o	13	I	45	170	151	94	51	114	356 } 419
	B-10	82	45	216	74	15	9	6	7	
10. vii	10-o	..	..	I	5	14	22	70	545	657 } 1111
	U.H. B-o	79	36	125	64	36	50	105	1058	
17. vii	B-10	48	50	63	74	87	66	34	35	457 } 1553
	10-o	I	..	4	..	6	4	10	108	
24. vii	B-10	64	42	62	42	22	18	I	22	273 } 590
	10-o	..	..	..	..	..	I	5	209	

TABLE VI (cont.)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
24. vii	U.H. B-o	100	70	135	80	68	48	25	188	714
31. vii	B-10	76	46	62	106	189	112	33	48	672
	10-o	1	4	6	15	24	30	57	625	762
31. vii	U.H. B-o	106	60	93	103	173	124	69	535	1263
7. viii	B-10	13	8	5	3	2	1	..	4	36
	10-o	2	..	2	14	13	31	23	115	200
	B-10	1	..	2	..	..	..	1	56	60
14. viii	10-o	..	..	..	1	1	1	11	595	609
14. viii	U.H. B-o	9	6	21	26	14	13	10	475	574
21. viii	B-10	1	3	3	6	23	11	3	15	65
	10-o	1	5	3	6	15	17	17	28	92
27. viii	U.H. B-o	6	11	16	27	54	90	50	110	364
28. viii	† B-o	12	15	98	34	19	18	19	177	392
1. ix	† B-o	8	6	9	11	8	15	32	126	215
2. x	* B-o	..	..	5	9	5	10	8	108	145

* One undivided haul.

‡ Average of five undivided hauls.

† Average of two undivided hauls.

+ Present, but less than 0.5 per haul.

|| Average of four undivided hauls.

TABLE VII. *TEMORA LONGICORNIS*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
17. i	B-o	..	..	..	..	..	..	..	20	20
23. i	B-o	..	..	..	..	..	..	..	22	22
31. i	B-o	..	..	..	..	..	+	+	18	19
7. ii	B-o	..	..	..	..	+	..	+	26	27
13. ii	B-o	..	..	..	..	+	..	1	65	66
20. ii	B-o	..	..	..	..	+	+	2	122	125
27. ii	B-o	..	+	..	1	..	1	1	167	171
7. iii	B-o	+	+	+	1	2	4	9	222	238
13. iii	B-o	..	..	1	1	4	2	4	74	86
20. iii	† B-o	..	1	+	+	1	4	13	117	136
27. iii	B-10	..	..	1	1	3	1	1	29	36
	10-o	2	4	2	6	32	9	13	102	170
4. iv	B-10	..	2	..	2	2	4	1	70	81
	10-o	3	7	1	3	10	9	14	382	429
10. iv	B-10	..	2	2	..	..	1	..	135	140
	10-o	85	68	45	28	28	22	88	1390	1754
17. iv	B-10	..	1	3	..	1	4	1	238	248
	10-o	26	27	18	15	27	34	47	2240	2434
24. iv	B-10	2	2	..	..	..	..	..	67	71
	10-o	9	10	11	17	23	20	50	485	625
24. iv	† U.H. B-o	38	13	18	15	8	10	43	408	553
1. v	B-10	21	6	1	3	9	24	16	187	267
	10-o	43	27	35	31	64	138	95	600	1033
8. v	B-10	..	..	..	..	..	..	..	46	46
	10-o	71	53	60	42	26	12	16	660	940
8. v	† U.H. B-o	37	23	29	30	13	10	1	156	299
15. v	† B-o	11	6	11	3	1	1	..	88	121
22. v	B-10	..	1	..	..	..	..	..	60	61
	10-o	52	12	14	1	1	1	6	236	323
22. v	† U.H. B-o	15	14	7	5	1	1	4	140	187
29. v	B-10	1	..	..	..	..	..	..	83	84
	10-o	..	1	2	1	2	2	19	504	531
5. vi	B-10	..	..	..	..	..	..	..	11	11
	10-o	..	2	4	11	9	10	27	318	381

TABLE VII (cont.)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
5. vi	‡U.H. B-o	11	3	7	7	4	12	10	440	494
12. vi	{B-10	1	..	..	..	..	1	1	13	16}
	{10-0	9	2	4	5	7	15	33	434	509}
19. vi	{B-10	..	..	1	4	3	2	..	17	27}
	{10-0	4	4	6	11	19	10	6	67	127}
19. vi	*B-o	2	8	6	1	6	4	3	162	192
19. vi	*B-o	8	8	12	13	9	10	5	77	142
19. vi	*B-o	13	12	17	18	16	19	9	103	207
26. vi	{B-10	..	1	..	1	..	..	1	11	14}
	{10-0	..	..	..	..	1	2	11	144	158}
26. vi	*B-o	4	2	6	2	..	..	5	60	79
26. vi	*B-o	3	2	2	1	1	5	11	57	82
26. vi	*B-o	4	1	1	5	2	3	10	67	93
26. vi	*B-o	1	1	2	2	2	6	1	58	73
3. vii	{B-10	6	3	2	5	..	..	1	8	25}
	{10-0	1	..	..	4	2	15	26	650	698}
3. vii	‡U.H. B-o	16	12	14	26	24	26	25	520	663
10. vii	{B-10	33	32	20	3	2	1	2	9	102}
	{10-0	..	..	2	5	10	20	32	290	359}
10. vii	‡U.H. B-o	31	24	28	19	28	54	79	1238	1501
17. vii	{B-10	23	17	27	24	23	20	11	37	182}
	{10-0	..	..	1	2	4	3	10	264	284}
24. vii	{B-10	24	19	14	14	14	2	3	23	113}
	{10-0	..	1	1	4	6	24	27	234	297}
24. vii	‡U.H. B-o	21	18	48	38	28	35	38	428	654
31. vii	{B-10	22	10	24	14	10	12	9	92	193}
	{10-0	2	4	1	12	18	23	49	294	403}
31. vii	‡U.H. B-o	36	23	22	22	28	26	30	292	479
7. viii	{B-10	14	5	9	1	1	1	2	13	46}
	{10-0	1	1	5	12	30	65	133	645	892}
14. viii	{B-10	1	..	2	..	1	2	1	38	45}
	{10-0	1	1	6	26	69	79	103	870	1155}
14. viii	‡U.H. B-o	13	15	22	27	54	56	51	320	558
21. viii	{B-10	7	6	6	7	4	5	7	109	151}
	{10-0	2	..	5	18	32	64	66	520	707}
21. viii	‡U.H. B-o	16	21	19	23	49	45	65	545	783
28. viii	‡B-o	27	32	14	14	23	27	71	1130	1338
11. ix	§B-o	12	7	5	7	7	18	28	175	259
2. x	*B-o	9	3	5	6	8	17	20	146	214

+ Present, but less than 0.5 per haul.

* One undivided haul.

† Average of two undivided hauls.

‡ Average of four undivided hauls.

§ Average of five undivided hauls.

TABLE VIII. *ACARTIA CLAUSI*. NUMBER PER HAUL

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
17. i	§B-o	1	4	..	..	+	..	..	5	10
23. i	‡B-o	+	6	+	+	..	+	..	4	11
30. i	§B-o	+	3	..	..	..	..	..	9	12
6. ii	§B-o	..	3	..	..	..	..	..	16	19
13. ii	‡B-o	+	3	+	..	+	..	..	26	29
20. ii	§B-o	..	1	..	..	..	..	1	32	34
27. ii	§B-o	+	2	..	+	+	+	1	17	22
7. iii	‡B-o	+	1	+	+	1	2	2	30	37
13. iii	§B-o	..	1	..	..	..	1	1	6	9
20. iii	‡B-o	..	1	..	+	1	+	+	8	10
27. iii	{B-10	1	..	..	..	..	1	..	11	13}
	{10-0	..	..	2	..	2	3	..	14	21}

TABLE VIII (cont.)

Date	Haul, depth in m.	♂	♀	V	IV	III	II	I	N	Total
4. iv	B-10	..	..	..	..	..	..	..	2	2
	10-0	6	2	3	..	4	5	4	21	45
10. iv	B-10	..	..	..	..	..	..	..	10	10
	10-0	3	3	5	1	1	2	5	71	91
17. iv	B-10	..	..	..	..	..	1	..	4	5
	10-0	12	6	10	3	8	12	17	76	144
24. iv	B-10	2	1	1	..	..	..	..	8	12
	10-0	22	31	15	25	11	12	6	38	160
24. iv	‡U.H. B-0	5	20	8	13	10	8	5	23	92
1. v	B-10	5	5	..	..	..	..	1	26	37
	10-0	20	22	9	8	4	8	5	48	124
8. v	B-10	..	..	..	..	..	..	1	21	22
	10-0	25	19	5	2	5	5	15	107	183
8. v	‡U.H. B-0	14	10	1	2	..	..	3	31	61
15. v	†B-0	7	11	2	1	2	2	1	28	54
22. v	B-10	1	..	..	..	..	..	..	274	275
	10-0	26	13	24	6	3	..	9	234	315
22. v	‡U.H. B-0	20	12	5	6	1	1	4	278	327
29. v	B-10	..	..	..	..	..	1	..	220	221
	10-0	6	13	6	3	13	46	98	2460	2645
5. vi	B-10	..	..	..	..	..	..	2	168	170
	10-0	1	2	3	11	18	53	66	2030	2184
5. vi	‡U.H. B-0	4	7	10	14	20	23	46	1016	1140
12. vi	B-10	2	6	3	4	22	43	48	164	292
	10-0	32	31	43	81	151	300	264	2240	3142
19. vi	B-10	..	3	2	..	1	1	1	36	44
	10-0	4	12	8	15	33	23	19	320	434
19. vi	*B-0	23	22	28	29	38	44	44	258	486
19. vi	*B-0	19	7	20	26	41	35	30	258	436
19. vi	*B-0	35	29	45	40	40	48	39	240	516
26. vi	B-10	2	3	..	..	1	1	2	132	141
	10-0	2	..	..	1	3	2	24	1040	1072
26. vi	*B-0	9	19	7	9	10	10	21	525	610
26. vi	*B-0	25	34	22	18	13	19	26	555	712
26. vi	*B-0	41	32	24	15	22	19	20	830	1003
26. vi	*B-0	13	19	12	12	8	22	13	670	769
3. vii	B-10	63	36	36	15	8	4	12	730	904
	10-0	1	7	1	3	64	200	318	5390	5984
3. vii	‡U.H. B-0	222	174	99	83	106	210	510	7320	8724
10. vii	B-10	248	198	152	181	127	102	73	342	1423
	10-0	..	3	2	4	22	124	264	4540	4959
10. vii	‡U.H. B-0	286	149	244	340	333	392	776	5636	8156
17. vii	B-10	456	251	334	214	627	480	365	1795	4522
	10-0	2	2	1	11	13	60	187	2010	2286
24. vii	B-10	564	490	478	416	402	224	72	520	3166
	10-0	3	3	2	4	4	18	54	1295	1383
24. vii	‡U.H. B-0	1110	1450	1020	640	720	535	253	1430	7158
31. vii	B-10	485	510	800	590	362	208	114	560	3629
	10-0	10	15	22	40	77	238	298	1390	2090
31. vii	‡U.H. B-0	750	1130	1100	640	408	600	415	1280	6323
7. viii	B-10	368	238	162	120	46	12	5	111	1062
	10-0	3	1	5	18	87	165	234	1140	1653
14. viii	B-10	42	27	10	3	10	..	2	144	238
	10-0	1	..	1	5	44	92	154	2410	2707
14. viii	‡U.H. B-0	212	186	113	246	232	100	36	1350	2475
21. viii	B-10	280	262	163	86	37	18	11	212	1069
	10-0	3	4	18	118	254	362	77	1000	1836
21. viii	‡U.H. B-0	565	290	375	205	420	385	90	1700	4030
23. viii	†B-0	202	242	376	294	177	177	198	1360	3026
11. ix	§B-0	152	478	171	124	112	79	123	1370	2609
2. x	*B-0	114	324	296	480	500	565	264	1540	4083

-- Present, but less than 0.5 per haul.

* One undivided haul.

† Average of two undivided hauls.

‡ Average of four undivided hauls.

§ Average of five undivided hauls.

(For meaning of symbols see end of table)

Date	Haul, depth in m.	♂	♀	(For meaning of symbols see end of table)							Eggs	No. eggs per sac	Total*
				V	IV	III	II	I	N				
17. i	B-O	2	192	69	37	44	15	20	662	1150	5.9	1041	
23. i	B-O	4	210	64	22	16	19	24	956	1315	5.6	1315	
30. i	B-O	6	149	29	17	16	8	7	438	736	6.1	670	
6. ii	B-O	3	100	14	10	12	10	2	188	1472	6.7	339	
13. ii	B-O	3	113	31	9	9	12	12	418	926	7.1	607	
20. ii	B-O	2	152	25	14	12	19	25	486	1751	8.3	735	
27. iii	B-O	6	204	24	14	8	13	12	554	2038	8.8	835	
7. iii	B-O	5	268	25	14	14	17	25	864	3406	9.1	1232	
13. iii	B-O	2	164	8	8	10	8	15	320	2386	9.4	535	
20. iii	B-O	4	205	26	14	15	23	32	1030	2450	11.8	1349	
	B-O	..	26	5	2	1	..	7	237	545		278	
27. iii	B-O	4	21	12	11	11	9	27	520	329	13.1	893	
	B-O	2	60	31	2	5	15	10	104	1672		615	
4. iv	B-O	10	72	41	28	64	107	97	418	820	14.6	1029	
	B-O	2	29	3	2	5	5	7	233	462		286	
10. iv	B-O	22	55	39	67	62	55	33	292	593	14.0	911	
	B-O	4	26	12	2	2	7	21	236	602		625	
17. iv	B-O	33	91	130	86	36	47	43	1250	892	16.8	2026	
	B-O	5	32	7	1	2	4	6	146	888		310	
24. iv	B-O	32	79	79	45	36	70	73	1050	821	17.4	1667	
	B-O	43	173	75	33	30	73	93	819	3883	17.6	1339	
24. iv	B-O	24	141	62	63	89	68	845	2475	2475	13.6	3319	
1. v	B-O	48	52	63	82	144	174	126	1260	303		1949	
	B-O	1	1	1	1	1	2	..	51	152	12.2	62	
8. v	B-O	36	66	144	258	236	180	208	3900	413	12.6	5090	
8. v	B-O	29	135	89	128	127	102	92	780	1675		1482	
15. v	B-O	13	160	94	84	78	93	87	1070	1599	9.2	1683	
22. v	B-O	..	4	2	1	1	..	11	185	61	10.7	204	
	B-O	4	85	67	42	55	75	87	1050	798		1465	
22. v	B-O	13	165	100	69	71	99	149	1200	1573	11.1	1866	
29. v	B-O	2	47	9	6	3	3	30	360	894	15.5	3225	
	B-O	36	144	175	141	202	171	155	1740	2088		2765	
	B-O	8	34	7	10	10	16	13	236	691	17.2	334	
5. vi	B-O	..	11	21	29	50	60	51	2150	16		2372	
5. vi	B-O	44	196	196	101	91	132	106	2104	2406	18.4	2970	
	B-O	19	61	25	13	14	9	30	170	1461	17.2	341	
12. vi	B-O	20	94	82	65	58	68	86	2030	2230		2503	

19. vi	{B-10 {10-0	10	42	34	12	2	10	10	252	818	15.1	372	830
19. vi	{U.H. B-0 {U.H. B-0	9	34	19	14	11	10	5	356	550	14.6	458	1506
19. vi	{U.H. B-0 {U.H. B-0	42	174	70	36	53	40	51	1040	2872	14.3		1786
19. vi	{U.H. B-0 {U.H. B-0	63	304	127	85	56	36	45	960	3915	14.4		1058
26. vi	{B-10 {10-0	17	23	6	3	4	3	10	228	537	13.3	294	3310
26. vi	{U.H. B-0 {U.H. B-0	10	10	8	9	31	53	135	2760	50	13.8	3016	1449
26. vi	{U.H. B-0 {U.H. B-0	45	88	33	14	18	27	64	1160	1621	13.2		1780
26. vi	{U.H. B-0 {U.H. B-0	34	114	41	17	26	50	88	1410	2129	12.8		2443
26. vi	{U.H. B-0 {U.H. B-0	29	107	46	25	12	33	71	2120	1990	12.9		2177
3. vii	{B-10 {10-0	36	126	65	23	18	40	79	1790	2194	13.9	1241	11,156
3. vii	{U.H. B-0 {U.H. B-0	71	442	216	68	38	14	48	344	7980	13.3	9915	14,224
10. vii	{B-10 {10-0	10	37	53	129	326	675	1360	9560	20,680	13.0	2867	8427
10. vii	{U.H. B-0 {U.H. B-0	204	970	525	335	595	150	227	725	13,550	12.3	5560	18,069
10. vii	{U.H. B-0 {U.H. B-0	104	690	462	314	195	33	120	5320	24	14.2	8142	15,267
17. vii	{B-10 {10-0	141	934	1159	827	1226	1789	2104	9889	13,961	10.7	7125	10,086
24. vii	{B-10 {10-0	258	950	1585	1425	765	475	603	2080	13,650	10.6	4558	13,690
24. vii	{U.H. B-0 {U.H. B-0	2	2	10	29	70	324	780	5910	12	9.9	6743	11,092
31. vii	{B-10 {10-0	920	920	830	700	400	414	171	915	12,130	9.7	4349	10,090
31. vii	{U.H. B-0 {U.H. B-0	1	10	65	169	419	640	404	3820	59	7.6	1679	12,012
7. viii	{B-10 {10-0	310	1010	1520	1510	1790	1800	1010	4740	11,990	7.2	10,333	4682
14. viii	{B-10 {10-0	480	990	1300	535	340	368	220	2510	12,790	7.8	575	4897
14. viii	{U.H. B-0 {U.H. B-0	26	61	295	273	356	312	336	2690	108	8.7	6947	25,703
21. viii	{B-10 {10-0	290	1190	1590	1030	770	740	670	3810	11,840	8.9	18,756	26,575
21. viii	{U.H. B-0 {U.H. B-0	34	438	328	212	69	48	35	515	4080	7.1		31,403
28. viii	{B-10 {10-0	17	168	488	730	800	930	1070	6130	589	7.1		10,862
11. ix	{B-10 {10-0	4	57	66	29	20	12	23	364	491	8.0		8958
2. x	{U.H. B-0 {U.H. B-0	12	37	256	290	191	193	258	2870	49			
	{B-10 {10-0	31	490	545	595	350	224	212	2450	3158			
	{U.H. B-0 {U.H. B-0	83	510	455	505	390	360	404	4240	6490			
	{B-10 {10-0	67	382	627	1120	1480	2150	1810	11,120	13,450			
	{U.H. B-0 {U.H. B-0	225	1270	1430	1830	2330	1780	15350	15,350	13,450			
	{B-10 {10-0	133	1240	2000	3160	3010	2260	1500	18,100	6425			
	{U.H. B-0 {U.H. B-0	83	860	1470	1410	575	498	386	5580	4760			
	{B-10 {10-0	85	665	620	805	980	1450	770	3580	3940			

* Excluding eggs.

† One undivided haul.

‡ Average of two undivided hauls.

§ Average of four undivided hauls.

|| Average of five undivided hauls.

Stage	Date	No.	045/- 0539	0539- 0592	0644- 0696	0696- 0748	0748- 0800	0800- 0853	0853- 0905	0905- 0957	0957- 1009	1009- 1061	1061- 1114	1114- 1166	1166- 1218	1218- 1270	1270- 1322	1322- 1375	1375- 1427	Median size	
Q	12. vi	130	..	..	..	..	..	..	4	32	50	37	6	..	1	..	..	..	..	0.989	
	19. vi	104	..	..	..	..	..	..	6	23	30	28	14	..	..	..	..	..	..	0.999	
	26. vi	110	..	..	..	..	..	..	3	24	35	30	14	..	1	..	..	..	..	0.997	
	3. vii	116	..	..	..	..	..	..	9	39	34	21	10	..	..	..	..	..	..	0.970	
	10. vii	137	..	..	..	..	..	..	22	52	41	14	3	..	..	..	..	..	..	0.951	
	17. vii	98	..	..	..	..	..	..	18	34	23	17	4	..	..	..	..	..	..	0.901	
	17. vii	134	..	..	..	..	..	..	31	20	19	5	3	..	..	..	..	..	..	0.866	
	31. vii	113	..	..	..	..	..	..	30	20	7	2	2	..	..	..	..	..	..	0.868	
	7. viii	102	..	..	..	..	..	..	13	18	9	1	..	..	..	..	..	..	..	0.839	
	14. viii	125	..	..	..	..	..	..	8	12	10	6	4	..	..	..	..	..	..	0.803	
	21. viii	127	..	..	..	..	..	..	16	15	6	4	1	..	..	..	..	..	..	0.803	
	28. viii	102	..	..	..	..	..	..	14	9	4	3	..	..	..	..	..	..	..	0.820	
	11. ix	82	..	..	..	..	..	..	5	3	..	..	..	..	..	..	..	..	..	0.784	
	2. x	167	..	..	..	..	..	..	40	5	2	1	..	..	..	..	..	..	..	0.829	
	V	17. i	42	..	..	..	..	..	15	6	1	..	..	..	..	..	..	..	..	..	0.809
		23. i	33	..	..	..	..	..	4	3	..	..	..	..	..	..	..	..	..	..	0.765
		30. i	25	..	..	..	..	..	10	..	..	..	..	..	..	..	..	..	..	..	0.841
		6. ii	87	..	..	..	..	..	5	2	..	..	..	..	..	..	..	..	..	..	0.827
		13. ii	8	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	0.809
		27. ii	11	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	0.827
13. iii		9	..	..	..	..	..	5	8	1	..	..	..	..	..	..	..	..	..	0.870	
20. iii		18	..	..	..	..	..	..	11	11	15	8	..	..	..	..	..	..	..	0.864	
4. iv		45	..	..	..	..	..	..	7	5	10	1	..	..	..	..	..	..	..	0.974	
10. iv		23	..	..	..	..	..	2	7	6	26	7	..	..	..	..	..	..	..	0.957	
17. iv		50	..	..	..	..	..	9	23	13	9	3	..	..	..	..	..	..	..	0.914	
24. iv		51	..	..	..	..	..	20	31	20	10	2	1	..	..	..	..	..	..	0.900	
1. v		73	..	..	..	..	..	9	29	21	1	..	..	..	..	..	..	..	..	0.885	
8. v		62	..	..	..	..	..	10	16	4	2	..	..	..	..	..	..	..	..	0.843	
15. v		85	..	..	..	..	..	30	26	4	1	..	..	..	..	..	..	..	..	0.846	
22. v		87	..	..	..	..	..	50	19	4	1	..	..	..	..	..	..	..	..	0.816	
29. v		53	..	..	..	..	..	28	26	2	..	..	..	..	..	..	..	..	..	0.800	
5. vi		80	..	..	..	..	..	35	14	5	2	..	..	..	..	..	..	..	..	0.800	
12. vi		91	..	..	..	..	..	41	36	1	1	..	..	..	..	..	..	..	..	0.856	
19. vi		103	..	..	..	..	..	45	27	2	1	..	..	..	..	..	..	..	..	0.868	
26. vi	83	..	..	..	..	..	15	27	17	19	..	..	..	..	..	..	..	..	0.811		
3. viii	97	..	..	..	..	..	15	42	4	1	..	..	..	..	..	..	..	..	0.757		
10. viii	106	..	..	..	..	..	30	22	4	..	..	..	..	..	..	..	..	..	0.730		
17. viii	67	..	..	..	..	..	34	14	3	1	..	..	..	..	..	..	..	..	0.716		
24. viii	103	..	..	..	..	..	6	10	2	2	..	..	..	..	..	..	..	..	0.847		
31. viii	73	..	..	..	..	..	5	14	14	1	..	..	..	..	..	..	..	..	0.862		
7. xii	84	..	..	..	..	..	18	30	17	..	..	..	..	..	..	..	..	..	0.740		
14. xii	115	..	..	..	..	..	36	19	18	..	..	..	..	..	..	..	..	..	0.714		
21. xii	74	..	..	..	..	..	7	12	5	1	..	..	..	..	..	..	..	..	0.837		
28. xii	58	..	..	..	..	..	10	13	5	1	..	..	..	..	..	..	..	..	0.822		
11. x	60	..	..	..	..	..	8	17	5	1	..	..	..	..	..	..	..	..	0.808		
2. x	60	..	..	..	..	..	16	14	5	..	..	..	..	..	..	..	..	..	0.790		
V	17. i	88	..	..	..	..	20	31	18	..	..	..	..	..	..	..	..	..	..	0.836	
	23. i	79	..	..	..	..	32	22	11	3	..	..	..	..	..	..	..	..	..	0.831	
	30. i	44	..	..	..	..	6	22	14	..	..	..	..	..	..	..	..	..	..	0.827	
	6. ii	44	..	..	..	..	8	18	11	1	..	..	..	..	..	..	..	..	..	0.822	
	13. ii	9	..	..	..	..	2	2	3	..	..	..	..	..	..	..	..	..	..	0.822	

Stage	Date	No.	045/- 0539	0539- 0592	0644- 0696	0696- 0748	0748- 0800	0800- 0853	0853- 0905	0905- 0957	0957- 1009	1009- 1061	1061- 1114	1114- 1166	1166- 1218	1218- 1270	1270- 1322	1322- 1375	1375- 1427	Median size	
Q	12. vi	130	..	..	..	..	..	..	4	32	50	37	6	..	1	..	..	..	..	0.989	
	19. vi	104	..	..	..	..	..	2	6	23	30	28	14	..	..	..	..	..	..	0.999	
	26. vi	110	..	..	..	..	..	..	3	24	35	30	14	3	1	..	..	..	..	0.997	
	3. vii	116	..	..	..	..	..	..	9	39	34	21	10	3	..	..	..	..	..	0.970	
	10. vii	137	..	..	..	..	..	3	22	52	41	14	3	1	..	..	..	..	..	0.951	
	17. vii	98	..	..	..	..	..	..	18	34	23	17	4	1	..	..	..	..	..	0.901	
	17. vii	134	..	..	..	..	..	..	31	20	19	5	3	..	..	..	..	..	..	0.866	
	31. vii	113	..	..	..	..	..	..	30	20	7	2	2	..	..	..	..	..	..	0.868	
	7. viii	102	..	..	..	..	..	..	13	18	9	1	..	..	..	..	..	..	..	0.839	
	14. viii	125	..	..	..	..	..	..	8	12	10	6	4	..	..	..	..	..	..	0.803	
	21. viii	127	..	..	..	..	..	..	16	15	6	4	1	..	..	..	..	..	..	0.803	
	28. viii	102	..	..	..	..	..	..	14	9	4	3	..	..	..	..	..	..	..	0.820	
	11. ix	82	..	..	..	..	..	..	5	3	..	..	..	..	..	..	..	..	..	0.784	
	2. x	167	..	..	..	..	..	..	77	40	5	2	1	..	..	..	..	..	..	0.829	
	V	17. i	42	..	..	..	..	..	15	6	1	..	..	..	..	..	..	..	..	..	0.809
		23. i	33	..	..	..	..	..	4	3	..	..	..	..	..	..	..	..	..	..	0.765
		30. i	25	..	..	..	..	..	10	..	..	..	..	..	..	..	..	..	..	..	0.841
		6. ii	87	..	..	..	..	..	5	2	..	..	..	..	..	..	..	..	..	..	0.827
		13. ii	8	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	0.809
		27. ii	11	..	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..	..	0.827
13. iii		9	..	..	..	..	..	5	..	1	..	..	..	..	..	..	..	..	..	0.870	
20. iii		18	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	0.864	
4. iv		45	..	..	..	..	..	..	11	11	15	8	..	..	..	..	..	..	..	0.974	
10. iv		23	..	..	..	..	..	7	7	5	10	1	..	..	..	..	..	..	..	0.957	
17. iv		50	..	..	..	..	..	2	23	13	6	3	..	..	..	..	..	..	..	0.975	
24. iv		51	..	..	..	..	..	9	31	20	10	2	1	..	..	..	..	..	..	0.914	
1. v		73	..	..	..	..	..	20	29	21	9	..	..	..	..	..	..	..	..	0.900	
8. v		62	..	..	..	..	..	10	16	4	2	..	..	..	..	..	..	..	..	0.885	
15. v		85	..	..	..	..	..	30	26	4	1	..	..	..	..	..	..	..	..	0.843	
22. v		87	..	..	..	..	..	50	29	4	1	..	..	..	..	..	..	..	..	0.846	
29. v		53	..	..	..	..	..	28	16	2	..	..	..	..	..	..	..	..	..	0.816	
5. vi		80	..	..	..	..	..	35	14	5	2	..	..	..	..	..	..	..	..	0.800	
12. vi		91	..	..	..	..	..	41	36	1	1	..	..	..	..	..	..	..	..	0.800	
19. vi		103	..	..	..	..	..	45	22	27	2	..	..	..	..	..	..	..	..	0.856	
26. vi	83	..	..	..	..	..	15	27	17	1	..	..	..	..	..	..	..	..	0.868		
3. vii	97	..	..	..	..	..	15	42	19	1	..	..	..	..	..	..	..	..	0.811		
10. vii	106	..	..	..	..	..	30	22	4	..	..	..	..	..	..	..	..	..	0.757		
17. vii	67	..	..	..	..	..	34	14	3	1	..	..	..	..	..	..	..	..	0.730		
24. vii	103	..	..	..	..	..	6	10	4	2	..	..	..	..	..	..	..	..	0.716		
31. vii	73	..	..	..	..	..	5	7	10	1	..	..	..	..	..	..	..	..	0.847		
7. viii	84	..	..	..	..	..	14	19	14	1	..	..	..	..	..	..	..	..	0.862		
14. viii	115	..	..	..	..	..	3	30	17	..	..	..	..	..	..	..	..	..	0.740		
21. viii	74	..	..	..	..	..	7	19	18	..	..	..	..	..	..	..	..	..	0.714		
28. viii	58	..	..	..	..	..	3	12	5	1	..	..	..	..	..	..	..	..	0.837		
11. ix	60	..	..	..	..	..	19	13	5	1	..	..	..	..	..	..	..	..	0.822		
2. x	..	..	..	..	..	..	8	14	5	..	..	..	..	..	..	..	..	..	..	0.808	
V	17. i	88	..	..	..	..	20	31	18	..	..	..	..	..	..	..	..	..	..	0.790	
	23. i	79	..	..	..	..	32	22	11	3	..	..	..	..	..	..	..	..	..	0.836	
	30. i	44	..	..	..	..	6	22	14	..	..	..	..	..	..	..	..	..	..	0.831	
	6. ii	44	..	..	..	..	8	18	11	1	..	..	..	..	..	..	..	..	..	0.827	
	13. ii	9	..	..	..	..	2	2	3	..	..	..	..	..	..	..	..	..	..	0.822	

TABLE X (contd.)

Stage	Date	No.	0.487-	0.539-	0.592-	0.644-	0.696-	0.748-	0.800-	0.853-	0.853-	0.905-	0.905-	0.957-	1.009-	1.061-	1.114-	1.114-	1.166-	1.218-	1.270-	1.322-	1.375-	1.427	Median size
♂ V	7. iii	21	..	..	..	..	..	3	13	4	..	..	..	1	..	..	..	..	..	..	..	..	..	..	0.828
	13. iii	18	..	..	..	..	..	3	6	5	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0.827
	20. iii	16	..	..	..	..	..	3	7	4	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0.820
	4. iv	38	..	..	..	..	..	..	1	1	5	..	..	..	..	..	..	..	..	..	..	..	..	..	1.023
	10. iv	23	..	..	..	..	..	..	2	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	1.009
	17. iv	35	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.042
	24. iv	55	..	..	..	..	..	..	..	5	14	..	..	..	..	..	..	..	..	..	..	..	..	..	0.973
	1. v	63	..	..	..	..	..	..	..	10	23	..	..	..	..	..	..	..	..	..	..	..	..	..	0.966
	8. v	60	..	..	..	..	..	..	..	15	35	..	..	..	..	..	..	..	..	..	..	..	..	..	0.927
	15. v	56	..	..	..	..	..	..	..	6	37	..	..	..	..	..	..	..	..	..	..	..	..	..	0.927
	22. v	81	..	..	..	..	..	..	..	3	36	..	..	..	..	..	..	..	..	..	..	..	..	..	0.906
	29. v	71	..	..	..	..	..	..	..	8	42	..	..	..	..	..	..	..	..	..	..	..	..	..	0.881
	5. vi	78	..	..	..	..	..	..	..	32	34	..	..	..	..	..	..	..	..	..	..	..	..	..	0.882
	12. vi	93	..	..	..	..	..	..	..	32	4	..	..	..	..	..	..	..	..	..	..	..	..	..	0.855
	19. vi	95	..	..	..	..	..	..	..	49	31	..	..	..	..	..	..	..	..	..	..	..	..	..	0.843
	26. vi	81	..	..	..	..	..	..	..	36	27	..	..	..	..	..	..	..	..	..	..	..	..	..	0.827
	3. vii	62	..	..	..	..	..	..	..	30	34	..	..	..	..	..	..	..	..	..	..	..	..	..	0.862
	10. vii	84	..	..	..	..	..	..	..	17	33	..	..	..	..	..	..	..	..	..	..	..	..	..	0.871
	17. vii	62	..	..	..	..	..	..	..	30	29	..	..	..	..	..	..	..	..	..	..	..	..	..	0.805
	24. vii	75	..	..	..	..	..	..	..	13	7	..	..	..	..	..	..	..	..	..	..	..	..	..	0.819
	31. vii	90	..	..	..	..	..	..	..	18	8	..	..	..	..	..	..	..	..	..	..	..	..	..	0.763
	7. viii	45	..	..	..	..	..	..	..	8	7	..	..	..	..	..	..	..	..	..	..	..	..	..	0.725
	14. viii	75	..	..	..	..	..	..	..	13	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0.806
	21. viii	101	..	..	..	..	..	..	..	19	5	..	..	..	..	..	..	..	..	..	..	..	..	..	0.835
	28. viii	55	..	..	..	..	..	..	..	11	23	..	..	..	..	..	..	..	..	..	..	..	..	..	0.760
	11. ix	79	..	..	..	..	..	..	..	10	16	..	..	..	..	..	..	..	..	..	..	..	..	..	0.755
	2. x	58	..	..	..	..	..	..	..	18	16	..	..	..	..	..	..	..	..	..	..	..	..	..	0.800
			..	..	..	..	..	..	..	21	10	..	..	..	..	..	..	..	..	..	..	..	..	..	0.816
			..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.789
	20. iii	12	..	..	..	..	..	..	..	3	8	..	..	..	..	..	..	..	..	..	..	..	..	..	0.792
	4. iv	24	..	..	..	..	..	..	..	24	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.820
	17. iv	52	..	..	..	..	..	..	..	24	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.785
	24. iv	57	..	..	..	..	..	..	..	15	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0.785
	1. v	95	..	..	..	..	..	..	..	23	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0.775
	8. v	79	..	..	..	..	..	..	..	19	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0.760
	15. v	57	..	..	..	..	..	..	..	39	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0.756
	22. v	66	..	..	..	..	..	..	..	18	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.755
	29. v	49	..	..	..	..	..	..	..	28	3	..	..	..	..	..	..	..	..	..	..	..	..	..	0.758
	5. vi	90	..	..	..	..	..	..	..	26	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.755
	12. vi	90	..	..	..	..	..	..	..	31	11	..	..	..	..	..	..	..	..	..	..	..	..	..	0.756
	19. vi	99	..	..	..	..	..	..	..	47	8	..	..	..	..	..	..	..	..	..	..	..	..	..	0.775
	26. vi	85	..	..	..	..	..	..	..	68	9	..	..	..	..	..	..	..	..	..	..	..	..	..	0.774
	3. vii	133	..	..	..	..	..	..	..	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.770
	10. vii	97	..	..	..	..	..	..	..	97	7	..	..	..	..	..	..	..	..	..	..	..	..	..	0.775
	17. vii	64	..	..	..	..	..	..	..	70	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.763
	24. vii	117	..	..	..	..	..	..	..	41	9	..	..	..	..	..	..	..	..	..	..	..	..	..	0.770
	31. vii	89	..	..	..	..	..	..	..	72	8	..	..	..	..	..	..	..	..	..	..	..	..	..	0.776
	7. viii	52	..	..	..	..	..	..	..	56	8	..	..	..	..	..	..	..	..	..	..	..	..	..	0.768
	14. viii	82	..	..	..	..	..	..	..	39	7	..	..	..	..	..	..	..	..	..	..	..	..	..	0.759
	21. viii	79	..	..	..	..	..	..	..	10	66	..	..	..	..	..	..	..	..	..	..	..	..	..	0.753
	28. viii	92	..	..	..	..	..	..	..	12	48	..	..	..	..	..	..	..	..	..	..	..	..	..	0.762
	11. ix	81	..	..	..	..	..	..	..	20	48	..	..	..	..	..	..	..	..	..	..	..	..	..	0.752
	2. x	89	..	..	..	..	..	..	..	19	57	..	..	..	..	..	..	..	..	..	..	..	..	..	0.752
			..	..	..	..	..	..	..	2	46	..	..	..	..	..	..	..	..	..	..	..	..	..	0.752

♂ IV

[illegible]

TABLE XI. SIZE OF *PARACALANUS PARVUS* IN MM.

Stage	Date	No.	0.383- 0.418	0.418- 0.452	0.452- 0.487	0.487- 0.522	0.522- 0.557	0.557- 0.592	0.592- 0.626	0.626- 0.661	0.661- 0.696	0.696- 0.731	0.731- 0.766	0.766- 0.800	0.800- 0.835	0.835- 0.887	Median size
♂	17. vii-14. viii	13	..	..	..	..	..	..	..	..	1	6	6	..	..	..	0.730
	21. viii	21	..	..	..	..	..	..	..	..	1	6	11	..	..	..	0.745
	28. viii	75	..	..	..	..	..	..	..	..	..	17	33	24	1	..	0.753
	11. ix	84	..	..	..	..	..	..	..	..	..	21	49	12	..	..	0.747
♀	2. x	10	..	..	..	..	..	..	..	..	..	..	1	8	1	..	0.785
	17 and 24. vii	13	..	..	..	..	..	1	1	..	6	2	3	1	..	..	0.696
	31. vii	24	..	..	..	..	1	3	3	12	7	1	..	..	..	..	0.671
	7. viii	24	..	..	..	..	..	1	1	10	10	3	..	..	..	..	0.664
♂	14. viii	19	..	..	..	..	..	..	..	4	7	5	2	..	..	..	0.678
	21. viii	21	..	..	..	..	..	..	..	4	6	10	..	1	..	..	0.700
	28. viii	113	..	..	..	..	..	..	..	11	49	39	9	1	2	2	0.694
	11. ix	93	..	..	..	..	..	5	5	21	40	23	1	2	1	..	0.683
♀	2. x	70	..	..	..	..	..	..	..	..	8	34	25	3	..	..	0.725
	31. vii	22	..	..	..	..	..	..	..	3	9	8	2	..	..	..	0.695
	7 and 14. viii	16	..	..	..	..	..	..	..	2	6	7	1	..	..	..	0.698
	21. viii	29	..	..	..	..	..	..	..	..	7	14	8	..	..	..	0.710
♂	28. viii	50	..	..	..	..	..	..	..	..	3	26	20	1	..	..	0.726
	11. ix	30	..	..	..	..	..	..	..	1	3	19	7	..	..	..	0.720
	2. x	50	..	..	..	..	..	..	..	1	4	12	18	15	..	..	0.743
	17 and 24. vii	7	..	..	..	..	1	4	2	..	..	..	..	..	..	..	..
♀	31. vii	36	..	..	..	..	1	17	13	5	..	..	..	..	..	..	0.593
	7 and 14. viii	13	..	..	..	..	1	6	6	..	..	..	..	..	..	..	0.591
	21. viii	52	..	..	..	..	1	9	29	12	1	..	..	..	..	..	0.615
	28. viii	37	..	..	..	..	3	3	17	12	4	1	..	..	..	..	0.625
♂	11. ix	52	..	..	..	..	4	20	22	22	5	..	1	..	..	..	0.629
	2. x	90	..	..	..	..	2	14	44	44	26	2	1	1	..	..	0.648
	31. vii	53	..	..	..	2	15	34	2	..	..	..	..	..	..	..	0.565
	7 and 14. viii	7	..	..	..	1	2	4	..	..	..	..	..	..	..	..	..
♀	21. viii	51	..	..	..	..	5	32	14	..	..	..	..	..	..	..	0.581
	28. viii	40	..	..	..	..	1	20	19	..	..	..	..	..	..	..	0.591
	11. ix	50	..	..	..	1	4	25	20	..	..	..	..	..	..	..	0.587
	2. x	36	..	..	..	..	2	9	23	2	..	..	..	..	..	..	0.602
♀	17 and 24. vii	8	..	..	2	4	..	..	..	..	..	..	..	..	..	..	..
	31. vii	51	..	..	5	34	11	1	..	..	..	..	..	..	..	..	0.510
	7 and 14. viii	15	..	..	1	11	3	1	..	..	..	..	..	..	..	..	0.514
	21. viii	50	..	..	..	25	24	1	..	..	..	..	..	..	..	..	0.523
III	28. viii	40	..	..	1	14	3	1	..	..	..	..	..	..	..	..	0.530
	11. ix	85	..	..	15	15	56	14	..	..	..	..	..	..	..	..	0.538
	2. x	53	..	..	8	35	10	..	..	..	..	..	..	..	..	..	0.542
	17 and 24. vii	13	1	5	7	..	..	..	..	..	..	..	..	..	..	..	0.455
III	31. vii	90	..	37	47	6	..	..	..	..	..	..	..	..	..	..	0.458
	7. viii	39	..	17	22	..	..	..	..	..	..	..	..	..	..	..	0.456
	21. viii	20	..	13	16	..	..	..	..	..	..	..	..	..	..	..	0.455

TABLE XII. SIZE OF *MICROCALANUS PYGMAEUS* IN MM.

Stage	Date	No.	0.313- 0.348	0.348- 0.383	0.383- 0.418	0.418- 0.452	0.452- 0.487	0.487- 0.522	0.522- 0.557	0.557- 0.592	0.592- 0.626	0.626- 0.661	Median size
♂	23. i	18	..	..	..	..	I	3	14	..	..	..	0.533
	6. ii	29	..	..	..	..	..	4	25	..	..	..	0.535
	13. ii	30	..	..	..	..	..	7	21	2	..	..	0.540
	20. ii	110	..	..	..	..	..	10	85	15	..	..	0.538
	27. ii	13	..	..	..	..	..	..	10	3	..	..	0.546
	7. iii	67	..	..	..	..	..	2	51	14	..	..	0.548
	13. iii	81	..	..	..	..	..	I	56	24	..	..	0.551
	20. iii	90	..	..	..	..	..	2	48	40	..	..	0.554
	4. iv	42	..	..	..	..	..	I	19	22	..	..	0.558
	10. iv	85	..	..	..	..	..	5	47	32	I	..	0.552
	17. iv	19	..	..	..	..	..	..	5	14	..	..	0.574
	24. iv	43	..	..	..	..	..	..	12	29	2	..	0.566
	I. v	37	..	..	..	..	..	..	12	23	2	..	0.564
	8. v	55	..	..	..	..	..	..	23	31	I	..	0.561
	15. v	78	..	..	..	..	..	I	53	24	..	..	0.550
	22. v	109	..	..	..	..	..	7	93	9	..	..	0.541
	29. v	42	..	..	..	..	..	I	26	15	..	..	0.551
	5. vi	54	..	..	..	..	..	..	39	15	..	..	0.549
	12. vi	27	..	..	..	..	..	I	17	9	..	..	0.552
	26. vi	56	..	..	..	..	..	5	44	7	..	..	0.540
	3. vii	95	..	..	..	..	..	17	72	6	..	..	0.533
	10. vii	75	..	..	..	..	..	23	52	..	..	..	0.529
	17. vii	47	..	..	..	..	..	8	31	8	..	..	0.539
	24. vii	22	..	..	..	..	..	4	18	..	..	..	0.531
	31. vii	20	..	..	..	..	..	6	14	..	..	..	0.530
	7. viii	27	..	..	..	..	..	9	18	..	..	..	0.529
	14. viii	28	..	..	..	..	..	15	13	..	..	..	0.522
♀	17. i	35	..	..	..	..	..	9	24	2	..	..	0.533
	23. i	64	..	..	..	..	..	15	46	3	..	..	0.535
	30. i	26	..	..	..	..	..	14	11	I	..	..	0.521
	6. ii	93	..	..	..	..	..	26	60	7	..	..	0.532
	13. ii	67	..	..	..	..	..	6	54	7	..	..	0.539
	20. ii	59	..	..	..	..	..	4	33	21	I	..	0.550
	27. ii	105	..	..	..	..	..	6	53	45	I	..	0.552
	7. iii	71	..	..	..	..	..	I	18	47	5	..	0.566
	13. iii	74	..	..	..	..	..	..	15	50	9	..	0.571
	20. iii	76	..	..	..	..	..	2	14	46	14	..	0.574
	27. iii	27	..	..	..	..	..	..	9	16	2	..	0.568
	4. iv	69	..	..	..	..	..	I	11	31	25	I	0.583
	10. iv	122	..	..	..	..	..	I	16	72	32	I	0.581
	17. iv	78	..	..	..	..	..	..	12	49	17	..	0.580
	24. iv	89	..	..	..	..	..	..	9	50	30	..	0.584
	I. v	88	..	..	..	..	..	..	7	52	28	I	0.584
	8. v	102	..	..	..	..	..	2	23	65	11	I	0.570
	15. v	105	..	..	..	..	..	..	26	67	11	I	0.569
	22. v	103	..	..	..	..	..	I	63	36	3	..	0.551
	29. v	157	..	..	..	..	..	I	61	79	16	..	0.562
	5. vi	126	..	..	..	..	..	3	64	49	10	..	0.555
	12. vi	88	..	..	..	..	..	3	33	43	9	..	0.562
	19. vi	118	..	..	..	..	..	..	58	49	11	..	0.558
	26. vi	115	..	..	..	..	..	2	33	65	15	..	0.567
	3. vii	129	..	..	..	..	..	8	61	55	5	..	0.555
	10. vii	101	..	..	..	..	..	7	47	41	5	I	0.555
	17. vii	112	..	..	..	..	..	5	42	58	6	I	0.561
	24. vii	62	..	..	..	..	..	8	39	14	I	..	0.542
	31. vii	92	..	..	..	..	..	16	59	17	..	..	0.541
	7. viii	81	..	..	..	..	..	31	40	9	I	..	0.529
	14. viii	82	..	..	..	..	..	26	45	10	I	..	0.533
	21. viii	97	..	..	..	..	I	43	44	9	..	..	0.525
	28. viii	63	..	..	..	..	2	31	26	3	I	..	0.522
	11. ix	78	..	..	..	..	I	38	37	2	..	..	0.522
	2. x	29	..	..	..	..	I	22	6	..	..	..	0.511
104	17. i	20	..	..	..	..	4	15	I	..	..	..	0.497
	23. i	71	..	..	..	..	I	59	11	..	..	..	0.508
	30. i	20	..	..	..	..	2	14	4	..	..	..	0.513
	6. ii	57	..	..	..	..	2	38	16	I	..	..	0.516
	13. ii	42	..	..	..	..	..	22	20	..	..	..	0.522
	20. ii	42	..	..	..	..	..	23	19	..	..	..	0.521
	27. ii	72	..	..	..	..	I	38	33	..	..	..	0.521
	7. iii	61	..	..	..	..	..	16	43	2	..	..	0.532
	13. iii	43	..	..	..	..	..	7	32	4	..	..	0.433
	20. iii	53	..	..	..	..	..	5	41	7	..	..	0.541
	4. iv	22	..	..	..	..	..	2	18	2	..	..	0.539
	10. iv	58	..	..	..	..	..	3	45	10	..	..	0.546
	17. iv	36	..	..	..	..	..	2	25	9	..	..	0.549
	24. iv	56	..	..	..	..	..	4	44	8	..	..	0.546
	I. v	75	..	..	..	..	..	9	57	9	..	..	0.542

TABLE XII (cont.)

Stage	Date	No.	0.313- 0.348	0.348- 0.383	0.383- 0.418	0.418- 0.452	0.452- 0.487	0.487- 0.522	0.522- 0.557	0.557- 0.592	0.592- 0.626	0.626- 0.661	Median size
♂ V	22. v	48	..	..	..	..	..	15	32	I	..	..	0.530
	29. v	33	..	..	..	..	..	5	26	2	..	..	0.534
	5. vi	13	..	..	..	..	..	..	10	3	..	..	0.534
	12. vi	56	..	..	..	..	..	6	48	2	..	..	0.535
	19. vi	28	..	..	..	..	..	5	23	..	..	..	0.534
	26. vi	66	..	..	..	I	4	42	19	..	..	..	0.514
	3. vii	66	..	..	..	..	3	43	20	..	..	..	0.513
	10. vii	79	..	..	..	..	3	53	23	..	..	..	0.514
	17. vii	62	..	..	..	..	..	37	25	..	..	..	0.519
	24. vii	53	..	..	..	..	..	29	24	..	..	..	0.520
	31. vii	69	..	..	..	..	..	51	18	..	..	..	0.515
	7. viii	26	..	..	..	..	3	21	2	..	..	..	0.500
	14. viii	31	..	..	..	I	4	24	2	..	..	..	0.503
	28. viii	15	..	..	..	..	4	11	..	..	..	..	0.497
	11. ix	13	..	..	..	..	3	10	..	..	..	..	0.499
♀ V	17. i	10	..	..	..	4	6	..	..	..	..	..	0.456
	23. i	79	..	..	..	9	64	5	I	..	..	..	0.465
	30. i	15	..	..	..	5	9	I	..	..	..	..	0.459
	6. ii	46	..	..	..	5	36	5	..	..	..	..	0.467
	13. ii	35	..	..	..	4	28	3	..	..	..	..	0.468
	20. ii	57	..	..	..	6	41	10	..	..	..	..	0.474
	27. ii	27	..	..	..	2	23	2	..	..	..	..	0.469
	7. iii	52	..	..	..	..	30	22	..	..	..	..	0.485
	13. iii	42	..	..	..	I	9	30	I	I	..	..	0.497
	20. iii	31	..	..	..	..	9	20	2	..	..	..	0.495
	4. iv	17	..	..	..	..	3	11	3	..	..	..	0.508
	10. iv	38	..	..	..	..	2	33	3	..	..	..	0.508
	17. iv	29	..	..	..	..	I	24	4	..	..	..	0.511
	24. iv	36	..	..	..	..	I	31	4	..	..	..	0.509
	1. v	50	..	..	..	..	6	38	6	..	..	..	0.503
	8. v	40	..	..	..	..	9	28	3	..	..	..	0.497
	15. v	59	..	..	..	..	34	25	..	..	..	..	0.485
	22. v	86	..	..	..	I	35	48	2	..	..	..	0.490
	29. v	12	..	..	..	..	I	8	3	..	..	..	0.499
	5. vi	22	..	..	..	I	4	17	..	..	..	..	0.496
	12. vi	56	..	..	..	..	16	38	2	..	..	..	0.495
	19. vi	41	..	..	..	I	17	20	3	..	..	..	0.490
	26. vi	87	..	..	..	17	62	8	..	..	..	..	0.464
	3. vii	53	..	..	..	13	39	I	..	..	..	..	0.461
	10. vii	69	..	..	..	13	56	..	..	..	..	..	0.462
	17. vii	60	..	..	..	4	44	11	I	..	..	..	0.476
	24. vii	49	..	..	..	I	43	5	..	..	..	..	0.473
	31. vii	82	..	..	..	15	63	4	..	..	..	..	0.462
	7. viii	28	..	..	..	10	18	..	..	..	..	..	0.457
	14. viii	48	..	..	..	23	25	..	..	..	..	..	0.453
	11. ix	11	..	..	..	5	6	..	..	..	..	..	0.455
♂ IV	17. i	34	..	..	14	20	..	..	..	..	..	..	0.422
	23. i	43	..	..	9	33	I	..	..	..	..	..	0.429
	30. i	23	..	..	19	4	..	..	..	..	..	..	0.410
	6. ii	45	..	..	17	28	..	..	..	..	..	..	0.422
	13. ii	38	..	..	9	29	..	..	..	..	..	..	0.426
	20. ii	61	..	..	5	55	I	..	..	..	..	..	0.432
	27. ii	55	..	..	8	46	I	..	..	..	..	..	0.430
	7. iii	32	..	..	..	31	I	..	..	..	..	..	0.438
	13. iii	38	..	..	..	35	3	..	..	..	..	..	0.439
	20. iii	14	..	..	..	8	6	..	..	..	..	..	0.451
	4. iv	23	..	..	..	13	10	..	..	..	..	..	0.451
	10. iv	41	..	..	2	22	17	..	..	..	..	..	0.450
	17. iv	27	..	..	..	8	18	I	..	..	..	..	0.459
	24. iv	60	..	..	..	29	31	..	..	..	..	..	0.453
	1. v	71	..	..	..	41	30	..	..	..	..	..	0.450
	8. v	57	..	..	..	25	32	..	..	..	..	..	0.454
	15. v	56	..	..	2	46	8	..	..	..	..	..	0.441
	22. v	16	..	..	2	12	2	..	..	..	..	..	0.443
	5. vi	13	..	..	..	10	3	..	..	..	..	..	0.447
	12. vi	57	..	..	3	39	15	..	..	..	..	..	0.445
	19. vi	33	..	..	3	26	4	..	..	..	..	..	0.435
	26. vi	38	..	..	9	29	..	..	..	..	..	..	0.425
	3. vii	51	..	..	18	33	..	..	..	..	..	..	0.424
	10. vii	47	..	..	11	36	..	..	..	..	..	..	0.427
	17. vii	45	..	..	..	41	3	..	..	..	..	..	0.439
	24. vii	32	..	..	3	29	..	..	..	..	..	..	0.428
	31. vii	19	..	..	9	10	..	..	..	..	..	..	0.420
	7. viii	12	..	..	4	8	..	..	..	..	..	..	0.425
	14. viii	10	..	..	5	5	..	..	..	..	..	..	0.420

TABLE XII (cont.)

Stage	Date	No.	0.313- 0.348	0.348- 0.383	0.383- 0.418	0.418- 0.452	0.452- 0.487	0.487- 0.522	0.522- 0.557	0.557- 0.592	0.592- 0.626	0.626- 0.661	Median size
♀ IV	17. i	40	..	7	32	I	..	..	..	..	..	..	0.394
	23. i	68	..	I	65	2	..	..	..	..	..	..	0.398
	30. i	12	..	7	5	..	..	..	..	..	..	..	0.381
	6. ii	32	..	6	26	..	..	..	..	..	..	..	0.393
	13. ii	36	..	2	34	..	..	..	..	..	..	..	0.400
	20. ii	48	..	2	42	4	..	..	..	..	..	..	0.404
	27. ii	35	..	..	30	5	..	..	..	..	..	..	0.402
	7. iii	28	..	I	26	I	..	..	..	..	..	..	0.406
	13. iii	42	..	..	24	18	..	..	..	..	..	..	0.415
	20. iii	11	..	..	7	4	..	..	..	..	..	..	0.413
	4. iv	30	..	..	4	26	..	..	..	..	..	..	0.427
	10. iv	39	..	..	I	38	..	..	..	..	..	..	0.428
	17. iv	23	..	..	4	17	2	..	..	..	..	..	0.438
	24. iv	61	..	..	11	47	3	..	..	..	..	..	0.427
	1. v	63	..	..	15	46	2	..	..	..	..	..	0.427
	8. v	38	..	..	9	28	I	..	..	..	..	..	0.427
	15. v	51	..	..	31	19	I	..	..	..	..	..	0.414
	22. v	25	..	..	14	11	..	..	..	..	..	..	0.416
	5. vi	14	..	..	3	11	..	..	..	..	..	..	0.427
	12. vi	59	..	..	18	41	..	..	..	..	..	..	0.424
	19. vi	41	..	I	24	14	2	..	..	..	..	..	0.414
	26. vi	75	..	5	67	3	..	..	..	..	..	..	0.397
	3. vii	69	..	13	55	I	..	..	..	..	..	..	0.392
	10. vii	70	..	3	62	5	..	..	..	..	..	..	0.399
	17. vii	69	..	I	48	20	..	..	..	..	..	..	0.410
	24. vii	41	..	2	37	2	..	..	..	..	..	..	0.398
	31. vii	37	..	9	27	I	..	..	..	..	..	..	0.393
	7. viii	18	..	4	13	I	..	..	..	..	..	..	0.395
	14. viii	8	..	2	6	..	..	..	..	..	..	..	0.392
III	17. i	71	22	49	..	..	..	..	..	..	..	..	0.354
	23. i	33	18	15	..	..	..	..	..	..	..	..	0.347
	30. i	19	12	7	..	..	..	..	..	..	..	..	0.345
	6. ii	56	22	34	..	..	..	..	..	..	..	..	0.352
	13. ii	137	75	62	..	..	..	..	..	..	..	..	0.347
	20. ii	68	19	48	I	..	..	..	..	..	..	..	0.355
	27. ii	83	39	44	..	..	..	..	..	..	..	..	0.350
	7. iii	50	13	37	..	..	..	..	..	..	..	..	0.355
	13. iii	46	4	38	4	..	..	..	..	..	..	..	0.367
	20. iii	19	I	16	I	I	..	..	..	..	..	..	0.362
	27. iii	59	3	56	..	..	..	..	..	..	..	..	0.361
	4. iv	64	5	52	7	..	..	..	..	..	..	..	0.370
	10. iv	53	5	40	8	..	..	..	..	..	..	..	0.367
	17. iv	72	..	54	17	I	..	..	..	..	..	..	0.376
	24. iv	63	..	49	14	..	..	..	..	..	..	..	0.375
	1. v	79	I	56	22	..	..	..	..	..	..	..	0.375
	8. v	75	4	66	5	..	..	..	..	..	..	..	0.369
	15. v	50	8	40	2	..	..	..	..	..	..	..	0.358
	22. v	24	2	20	2	..	..	..	..	..	..	..	0.369
	5. vi	41	3	35	3	..	..	..	..	..	..	..	0.362
	12. vi	57	4	47	6	..	..	..	..	..	..	..	0.367
	19. vi	36	7	28	I	..	..	..	..	..	..	..	0.359
	26. vi	67	35	32	..	..	..	..	..	..	..	..	0.348
	3. vii	56	29	27	..	..	..	..	..	..	..	..	0.348
	10. vii	82	41	41	..	..	..	..	..	..	..	..	0.348
	17. vii	61	19	40	2	..	..	..	..	..	..	..	0.357
	24. vii	22	13	9	..	..	..	..	..	..	..	..	0.346
	31. vii	35	19	16	..	..	..	..	..	..	..	..	0.347
	7. viii	17	7	10	..	..	..	..	..	..	..	..	0.352

TABLE XIII. SIZE OF CENTROPAGES HAMATUS IN MM.

Stage	Date	No.	0592- 0644	0644- 0696	0748- 0800	0800- 0853	0853- 0905	0905- 0957	0957- 1009	1009- 1061	1061- 1114	1114- 1166	1166- 1218	1218- 1270	1270- 1322	1322- 1375	1375- 1427	1427- 1479	1479- 1531	Median size
♂	10. iv	51	..	..	..	..	..	..	..	5	18	18	10	..	..	..	..	..	..	1.123
	17. iv	25	..	..	..	..	..	..	..	3	5	8	7	1	..	..	..	..	..	1.152
	24. iv	26	..	..	..	..	..	..	..	..	4	10	10	2	..	..	..	..	..	1.163
	1. v	52	..	..	..	..	..	..	..	..	7	26	16	1	..	..	..	..	..	1.152
	8. v	30	..	..	..	..	..	..	..	1	5	9	8	4	..	..	..	..	..	1.151
	15. v	29	..	..	..	..	..	..	..	1	7	10	7	1	..	..	..	..	..	1.131
	22. v	24	..	..	..	..	..	..	..	7	4	2	3	..	..	..	..	..	..	1.064
	29. v	22	..	..	..	..	..	..	..	8	3	4	..	..	..	..	..	..	..	1.046
	5. vi	36	..	..	..	..	2	2	7	13	9	3	..	..	..	..	..	..	..	1.045
	12. vi	46	..	..	..	..	9	19	14	36	6	1	1	..	..	..	..	..	..	1.010
	19. vi	112	..	..	..	..	5	19	6	6	2	2	..	..	..	..	..	..	..	1.018
	26. vi	26	..	..	..	..	3	11	14	2	..	..	..	..	..	..	..	..	..	1.002
	3. vii	45	..	..	..	..	9	7	11	14	2	..	..	..	..	..	..	..	..	0.867
	10. vii	138	..	..	7	43	63	21	3	..	..	1	..	..	..	..	..	..	..	0.863
	17. vii	61	..	..	7	13	25	9	2	..	..	..	..	..	..	..	..	..	..	0.806
	24. vii	90	..	..	33	25	14	6	..	2	1	..	..	..	..	..	..	..	..	0.816
	31. vii	175	..	..	50	77	19	10	..	2	1	..	..	..	..	..	..	..	..	0.795
	7. viii	103	..	..	56	25	6	..	5	3	1	..	..	..	..	..	..	..	..	0.850
	14. viii	33	..	..	12	11	2	..	3	..	..	..	..	..	..	..	..	..	..	0.866
21. viii	23	..	..	1	1	6	4	..	..	..	..	..	..	..	..	..	..	..	0.858	
28. viii	22	..	..	1	1	18	17	4	..	..	..	..	..	..	..	..	..	..	1.302	
11. ix	40	..	..	1	..	..	..	..	..	..	..	1	..	5	17	6	4	..	1.326	
♀	10. iv	33	..	..	..	..	..	..	..	..	..	..	1	2	4	5	1	1	..	1.374
	17. iv	15	..	..	..	..	..	..	..	..	..	..	1	2	3	7	9	3	..	1.367
	24. iv	25	..	..	..	..	..	..	..	..	..	..	..	1	11	17	14	1	..	1.335
	1. v	35	..	..	..	..	..	..	..	..	1	..	..	1	4	4	..	..	..	1.362
	8. v	8	..	..	..	..	..	..	..	..	..	1	..	2	2	7	2	3	..	1.265
	15. v	17	..	..	..	..	..	..	..	..	..	1	..	4	2	..	..	..	..	1.198
	22. v	10	..	..	..	..	..	..	..	1	1	3	4	3	1	1	2	..	..	1.205
	29. v	14	..	..	..	..	..	..	..	..	2	5	3	3	4	..	..	..	..	1.175
	5. vi	14	..	..	..	..	..	..	..	1	2	3	2	3	1	..	..	..	..	1.123
	12. vi	14	..	..	..	..	..	..	..	..	3	5	2	1	..	..	..	..	..	0.979
	19. vi	34	..	..	..	..	..	..	1	13	6	3	1	..	..	..	..	..	..	0.958
	3. vii	18	..	..	..	..	..	..	1	29	7	3	..	..	..	..	..	..	..	0.909
	10. vii	83	..	..	1	1	9	6	18	19	2	2	..	..	..	..	..	..	..	0.881
	17. vii	57	..	..	6	9	14	16	17	7	1	1	1	1	..	..	..	..	..	0.881
	24. vii	65	..	..	8	9	28	22	16	1	1	1	..	..	..	..	..	..	..	0.855
	31. vii	103	..	..	4	22	15	9	5	2	1	1	..	..	..	..	..	..	..	0.931
	7. viii	48	..	..	3	12	15	6	10	6	4	1	..	..	..	..	..	..	..	0.931
	14. viii	20	..	..	3	7	10	4	10	4	4	1	..	..	..	..	..	..	..	0.903
	21. viii	46	..	..	3	7	13	7	13	7	4	..	..	..	..	..	..	..	..	0.933
28. viii	30	..	..	..	..	3	7	7	10	..	..	..	..	..	..	..	..	..	0.933	
11. ix	23	..	..	..	..	..	..	7	5	7	..	..	..	..	..	..	..	..	0.933	
♀	4. iv	26	..	..	..	1	4	14	7	..	..	..	..	..	..	..	..	..	..	0.937
	10. iv	25	..	..	..	..	3	12	7	3	..	..	..	..	..	..	..	..	..	0.977
	17. iv	22	..	..	..	..	1	8	10	3	..	..	..	..	..	..	..	..	..	0.966
	24. iv	14	..	..	..	..	3	3	8	..	..	..	..	..	..	..	..	..	..	0.934
	1. v	30	..	..	..	..	5	15	9	1	..	..	..	..	..	..	..	..	..	0.920
	8. v	14	..	..	..	..	4	7	2	1	..	..	..	..	..	..	..	..	..	0.856
	15. v	14	..	..	1	6	7	..	..	..	..	..	..	..	..	..	..	..	..	0.890
	22. v	14	..	..	..	..	3	10	..	..	..	..	..	..	..	..	..	..	..	0.879
	29. v	11	..	..	..	..	5	2	..	1	..	..	..	..	..	..	..	..	..	0.848
	5. vi	26	..	..	1	11	11	1	..	..	..	..	..	..	..	..	..	..	..	0.837
	12. vi	9	..	..	3	6	4	..	..	..	..	..	..	..	..	..	..	..	..	0.753
	19. vi	7	..	..	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0.733
	26. vi	8	..	..	38	13	..	..	..	..	..	..	..	..	..	..	..	..	..	0.713
	3. vii	98	..	..	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0.695
	10. vii	185	..	..	52	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0.684
	17. vii	33	..	..	17	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0.675
	24. vii	81	..	..	24	4	..	..	..	..	..	..	..	..	..	..	..	..	..	0.675
	31. vii	83	..	..	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	0.675

[illegible]

TABLE XIV. SIZE OF TEMORA LONGICORNIS IN MM.

Stage	Date	No.	0.383- 0.435	0.435- 0.487	0.487- 0.539	0.539- 0.592	0.592- 0.644	0.644- 0.696	0.696- 0.748	0.748- 0.800	0.800- 0.853	0.853- 0.905	0.905- 0.957	0.957- 1.009	1.009- 1.061	1.061- 1.114	1.114- 1.166	1.166- 1.218	1.218- 1.270	1.270- 1.322	Median size
♂	10. iv	92	..	..	..	..	2	8	17	31	17	10	7	6	3	1	..	..	..	0.837	
	17. iv	24	..	..	..	..	1	..	2	2	10	6	6	3	1	1	..	..	..	0.898	
	24. iv	24	..	..	..	..	..	..	6	9	16	9	18	6	3	2	1	..	..	0.937	
	1. v	59	..	..	..	..	..	2	3	2	9	9	3	5	8	4	..	..	..	0.919	
	8. v	88	..	..	..	..	..	..	3	14	34	34	25	6	1	1	..	..	..	0.895	
	15. v	21	..	..	..	..	..	..	1	3	18	5	9	4	1	1	..	..	..	0.887	
	22. v	61	..	..	..	..	..	2	13	18	13	13	4	4	1	1	..	..	..	0.847	
	29. v	14	..	..	..	..	..	1	6	7	11	4	2	2	2	..	..	..	..	0.862	
	5. vi	29	..	..	..	..	..	..	1	3	3	3	..	..	..	..	..	..	..	0.803	
	12. vi	15	..	..	..	..	..	..	7	5	2	3	3	2	..	..	..	..	..	0.754	
	19. vi	24	..	..	..	..	..	..	3	3	3	..	..	..	..	..	..	..	..	0.803	
	26. vi	8	..	..	..	..	..	..	7	5	2	3	3	2	..	..	..	..	..	..	0.716
	3. vii	69	..	..	..	..	8	3	11	..	2	..	..	..	..	..	..	..	..	..	0.657
	10. vii	72	..	..	..	..	20	37	5	3	..	..	..	..	..	..	..	..	..	..	0.625
	17. vii	26	..	..	..	..	14	6	..	2	..	..	..	..	..	..	..	..	..	..	0.630
	24. vii	41	..	..	..	..	12	7	..	..	..	..	..	..	..	..	..	..	..	..	0.591
	31. vii	56	..	..	..	..	21	6	..	..	..	..	..	..	..	..	..	..	..	..	0.597
	7. viii	77	..	..	..	..	32	9	..	..	..	..	..	..	..	..	..	..	..	..	0.601
	14. viii	44	..	..	..	..	26	3	..	..	..	..	..	..	..	..	..	..	..	..	0.669
	21. viii	68	..	..	..	..	31	13	..	..	..	..	..	..	..	..	..	..	..	..	0.678
28. viii	51	..	..	..	..	23	12	3	2	..	..	..	..	..	..	..	..	..	..	0.635	
11. ix	54	..	..	..	..	9	23	15	7	..	..	..	..	..	..	..	..	..	..	0.922	
♀	10. iv	85	..	..	..	..	1	3	2	12	21	11	11	9	10	10	3	3	..	..	1.036
	17. iv	25	..	..	..	..	..	..	..	..	3	1	1	6	4	3	5	2	1	..	1.067
	24. iv	33	..	..	..	..	..	..	..	..	1	1	1	1	3	3	3	1	..	..	0.957
	1. v	33	..	..	..	..	..	..	..	..	3	3	9	5	3	1	1	1	..	..	0.960
	8. v	60	..	..	..	..	..	..	..	..	10	13	13	8	2	3	3	2	..	..	1.001
	15. v	10	..	..	..	..	..	..	..	..	1	5	2	4	1	1	1	..	..	..	0.853
	22. v	21	..	..	..	..	..	..	..	..	5	2	3	2	..	..	..	..	..	..	0.830
	29. v	14	..	..	..	..	..	..	..	..	6	6	3	1	..	..	..	..	..	..	0.817
	5. vi	13	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.844
	19. vi	23	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.757
	3. vii	37	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.657
	10. vii	57	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.635
	17. vii	13	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.630
	24. vii	26	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.611
	31. vii	35	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.604
	7. viii	64	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.615
	14. viii	56	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.657
	21. viii	80	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.708
	28. viii	58	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.638
	11. ix	32	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
♀	10. iv	55	..	..	..	..	1	3	20	17	12	2	1	1	..	..	..	..	..	..	0.809
	17. iv	12	..	..	..	..	..	..	..	4	6	2	1	..	..	..	..	..	..	..	0.781
	24. iv	10	..	..	..	..	..	..	..	7	7	2	..	..	..	..	..	..	..	..	0.772
	1. v	25	..	..	..	..	..	..	..	11	7	..	..	..	..	..	..	..	..	..	0.746
	8. v	41	..	..	..	..	..	..	..	14	5	..	..	..	..	..	..	..	..	..	0.657
	22. v	13	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.657
	5. vi	16	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.643
	19. vi	17	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.594
	3. vii	66	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.578
	10. vii	26	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.537
	17. vii	24	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.504
	24. vii	15	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.533
31. vii	24	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.516	
7. viii	60	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.522	
14. viii	47	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.575	
21. viii	40	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.586	
28. viii	13	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.522	

[illegible]

TABLE XV. SIZE OF ACARTIA CLAUSI IN MM.

Stage	Date	No.	0-487- 0-539	0-539- 0-592	0-592- 0-644	0-644- 0-696	0-696- 0-748	0-748- 0-800	0-800- 0-853	0-853- 0-905	0-905- 0-957	0-957- 1-009	1-009- 1-061	1-061- 1-114	1-114- 1-166	1-166- 1-218	1-218- 1-270	Median size
25	24. iv	25	..	..	..	..	..	..	..	..	..	21	4	..	..	..	..	0.987
26	24. iv	26	..	..	..	..	..	..	..	..	..	15	7	..	..	..	..	0.988
27	24. iv	27	..	..	..	..	..	..	..	..	..	18	10	..	..	..	..	0.994
28	24. iv	28	..	..	..	..	..	..	..	..	..	15	..	..	..	..	..	0.959
29	24. v	29	..	..	..	..	..	..	..	..	..	18	..	..	..	..	..	0.955
30	24. v	30	..	..	..	..	..	..	..	..	..	10	1	..	..	..	..	0.939
31	24. v	31	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	0.934
32	24. v	32	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..	0.893
33	24. vi	33	..	..	..	..	..	..	..	..	..	9	..	..	..	..	..	0.907
34	24. vi	34	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..	0.907
35	24. vi	35	..	..	..	..	..	..	..	..	..	15	..	..	..	..	..	0.889
36	24. vi	36	..	..	..	..	..	..	..	..	..	14	..	..	..	..	..	0.885
37	24. vi	37	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	0.887
38	24. vi	38	..	..	..	..	..	..	..	..	..	98	..	..	..	..	..	0.866
39	24. vi	39	..	..	..	..	..	..	..	..	..	12	..	..	..	..	..	0.853
40	24. vii	40	..	..	..	..	..	..	..	..	..	90	..	..	..	..	..	0.833
41	24. vii	41	..	..	..	..	..	..	..	..	..	29	..	..	..	..	..	0.827
42	24. vii	42	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	0.819
43	24. vii	43	..	..	..	..	..	..	..	..	..	3	..	..	..	..	..	0.828
44	24. vii	44	..	..	..	..	..	..	..	..	..	11	..	..	..	..	..	0.833
45	24. vii	45	..	..	..	..	..	..	..	..	..	9	..	..	..	..	..	0.828
46	24. vii	46	..	..	..	..	..	..	..	..	..	8	..	..	..	..	..	0.848
47	24. vii	47	..	..	..	..	..	..	..	..	..	71	..	..	..	..	..	0.870
48	24. vii	48	..	..	..	..	..	..	..	..	..	9	..	..	..	..	..	0.874
49	24. vii	49	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..	0.879
50	24. vii	50	..	..	..	..	..	..	..	..	..	72	..	..	..	..	..	0.882
51	24. vii	51	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	0.882
52	24. vii	52	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..	0.853
53	24. vii	53	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
54	24. vii	54	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.819
55	24. vii	55	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
56	24. vii	56	..	..	..	..	..	..	..	..	..	9	..	..	..	..	..	0.833
57	24. vii	57	..	..	..	..	..	..	..	..	..	6	..	..	..	..	..	0.828
58	24. vii	58	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.848
59	24. vii	59	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.870
60	24. vii	60	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.874
61	24. vii	61	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.879
62	24. vii	62	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.882
63	24. vii	63	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
64	24. vii	64	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
65	24. vii	65	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.819
66	24. vii	66	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
67	24. vii	67	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.833
68	24. vii	68	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
69	24. vii	69	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.848
70	24. vii	70	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.870
71	24. vii	71	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.874
72	24. vii	72	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.879
73	24. vii	73	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.882
74	24. vii	74	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
75	24. vii	75	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
76	24. vii	76	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.819
77	24. vii	77	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
78	24. vii	78	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.833
79	24. vii	79	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
80	24. vii	80	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.848
81	24. vii	81	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.870
82	24. vii	82	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.874
83	24. vii	83	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.879
84	24. vii	84	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.882
85	24. vii	85	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
86	24. vii	86	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
87	24. vii	87	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.819
88	24. vii	88	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
89	24. vii	89	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.833
90	24. vii	90	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
91	24. vii	91	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.848
92	24. vii	92	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.870
93	24. vii	93	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.874
94	24. vii	94	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.879
95	24. vii	95	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.882
96	24. vii	96	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
97	24. vii	97	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
98	24. vii	98	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.819
99	24. vii	99	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
100	24. vii	100	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.833
101	24. vii	101	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
102	24. vii	102	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.848
103	24. vii	103	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.870
104	24. vii	104	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.874
105	24. vii	105	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.879
106	24. vii	106	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.882
107	24. vii	107	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
108	24. vii	108	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853
109	24. vii	109	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.819
110	24. vii	110	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
111	24. vii	111	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.833
112	24. vii	112	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.828
113	24. vii	113	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.848
114	24. vii	114	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.870
115	24. vii	115	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.874
116	24. vii	116	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.879
117	24. vii	117	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.882
118	24. vii	118	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	0.853

[illegible]

III

TABLE XVI. SIZE OF *OITHONA SIMILIS* IN MM.

Stage	Date	No.	0.313- 0.348	0.348- 0.383	0.383- 0.418	0.418- 0.452	0.452- 0.487	0.487- 0.522	0.522- 0.557	0.557- 0.592	0.592- 0.626	0.626- 0.661	Median size
♂	20. ii	8	..	..	..	..	..	5	3	..	..	..	..
	27. ii	23	..	..	..	..	..	12	11	..	..	..	0.522
	7. iii	26	..	..	..	..	..	9	15	2	..	..	0.528
	13. iii	9	..	..	..	..	..	1	8	..	..	..	0.539
	20. iii	15	..	..	..	..	..	4	9	2	..	..	0.542
	4. iv	12	..	..	..	..	..	..	7	5	..	..	0.554
	10. iv	37	..	..	..	..	..	1	17	19	..	..	0.559
	17. iv	34	..	..	..	..	..	1	20	13	..	..	0.552
	24. iv	46	..	..	..	..	..	..	21	25	..	..	0.559
	1. v	65	..	..	..	..	..	2	41	22	..	..	0.550
	8. v	57	..	..	..	..	..	3	44	10	..	..	0.548
	15. v	19	..	..	..	..	..	4	10	5	..	..	0.532
	22. v	14	..	..	..	..	..	1	13	..	..	..	0.538
	29. v	32	..	..	..	..	..	4	27	1	..	..	0.537
	5. vi	49	..	..	..	..	..	3	37	9	..	..	0.542
	12. vi	94	..	..	..	..	..	5	65	24	..	..	0.548
	19. vi	82	..	..	..	..	..	3	67	12	..	..	0.546
	26. vi	90	..	..	..	..	..	14	75	1	..	..	0.534
	3. vii	85	..	..	..	..	..	36	49	..	..	..	0.525
	10. vii	91	..	..	..	..	..	21	70	..	..	..	0.531
	17. vii	115	..	..	..	..	..	22	92	1	..	..	0.530
	24. vii	88	..	..	..	..	..	50	38	..	..	..	0.520
	31. vii	95	..	..	..	..	..	72	23	..	..	..	0.516
	7. viii	46	..	..	..	..	5	40	1	..	..	..	0.499
	14. viii	40	..	..	..	..	6	33	1	..	..	..	0.496
	21. viii	68	..	..	..	..	6	61	1	..	..	..	0.500
	28. viii	67	..	..	..	..	37	30	..	..	..	..	0.486
	11. ix	71	..	..	..	..	11	60	..	..	..	..	0.498
	2. x	72	..	..	..	..	6	65	1	..	..	..	0.500
+0	17. i	123	..	..	..	..	3	49	67	4	..	..	0.525
	23. i	194	..	..	..	..	2	105	83	3	1	..	0.521
	30. i	126	..	..	..	..	4	66	55	1	..	..	0.518
	6. ii	97	..	..	..	..	..	35	60	2	..	..	0.528
	13. ii	83	..	..	..	..	2	54	23	4	..	..	0.517
	20. ii	67	..	..	..	..	1	26	34	6	..	..	0.526
	27. ii	88	..	..	..	..	..	32	50	6	..	..	0.529
	7. iii	71	..	..	..	..	..	30	34	7	..	..	0.526
	14. iii	73	..	..	..	..	..	23	40	10	..	..	0.530
	20. iii	69	..	..	..	..	..	21	37	8	3	..	0.534
	27. iii	39	..	..	..	..	..	16	16	7	..	..	0.528
	4. iv	126	..	..	..	..	..	31	52	30	13	..	0.539
	10. iv	69	..	..	..	..	1	12	29	12	15	..	0.546
	17. iv	105	..	..	..	..	1	7	35	21	40	1	0.574
	24. iv	82	..	..	..	..	..	3	6	34	38	1	0.590
	1. v	97	..	..	..	..	..	2	10	36	45	4	0.593
	8. v	85	..	..	..	..	1	3	15	35	30	1	0.581
	15. v	69	..	..	..	..	..	2	26	33	8	..	0.563
	22. v	77	..	..	..	..	..	4	23	32	16	2	0.569
	29. v	85	..	..	..	..	..	2	19	49	12	3	0.570
	5. vi	95	..	..	..	..	..	4	26	54	10	1	0.568
	12. vi	103	..	..	..	..	..	1	28	62	12	..	0.571
	19. vi	112	..	..	..	..	..	1	27	73	10	1	0.571
	26. vi	91	..	..	..	..	..	2	34	50	5	..	0.563
	3. vii	98	..	..	..	..	..	1	54	37	6	..	0.554
	10. vii	91	..	..	..	..	..	..	41	46	4	..	0.560
	17. vii	94	..	..	..	..	..	4	61	25	4	..	0.547
	24. vii	74	..	..	..	..	..	17	48	9	..	..	0.535
	31. vii	91	..	..	..	..	..	27	58	0	..	..	0.530
	7. viii	78	..	..	..	..	..	52	25	1	..	..	0.517
	14. viii	61	..	..	..	..	..	45	16	..	..	..	0.515
	21. viii	95	..	..	..	..	2	46	47	..	..	..	0.522
	28. viii	65	..	..	..	..	2	41	22	..	..	..	0.517
	11. ix	60	..	..	..	..	..	44	16	..	..	..	0.516
	2. x	65	..	..	..	..	..	39	25	1	..	..	0.519
V	17. i	53	..	..	..	5	28	19	1	..	..	..	0.480
	23. i	49	..	..	..	..	30	18	1	..	..	..	0.482
	30. i	27	..	..	..	1	11	13	2	..	..	..	0.494
	6. ii	12	..	..	..	..	4	6	2	..	..	..	0.496
	13. ii	18	..	..	..	1	5	10	2	..	..	..	0.506
	20. ii	54	..	..	..	..	8	23	23	..	..	..	0.512
	27. ii	88	..	..	..	3	22	42	21	..	..	..	0.501
	7. iii	95	..	..	..	1	12	48	32	2	..	..	0.515
	13. iii	39	..	..	..	..	8	11	19	1	..	..	0.524
	20. iii	93	..	..	..	..	9	43	37	4	..	..	0.519
	27. iii	13	..	..	..	..	3	3	6	1	..	..	0.539
	4. iv	26	..	..	..	..	..	3	16	7	..	..	0.546
	10. iv	36	..	..	..	..	1	10	18	7	..	..	0.540
	17. iv	132	..	..	..	..	1	14	75	42	..	..	0.546
	24. iv	66	..	..	..	..	4	34	27	1	..	..	0.536
	1. v	107	..	..	..	..	6	44	51	6	..	..	0.524
	8. v	87	..	..	..	..	20	34	32	1	..	..	0.514
	15. v	81	..	..	..	1	22	39	19	..	..	..	0.501

TABLE XVI (cont.)

Stage	Date	No.	0°313- 0°348	0°348- 0°383	0°383- 0°418	0°418- 0°452	0°452- 0°487	0°487- 0°522	0°522- 0°557	0°557- 0°592	0°592- 0°626	0°626- 0°661	Median size	
V	22. v	80	..	..	..	..	14	33	33	..	..	..	0°516	
	29. v	109	..	..	..	..	2	40	67	..	..	..	0°527	
	5. vi	101	..	..	..	..	3	46	51	I	..	..	0°523	
	12. vi	97	..	..	..	..	I	35	60	I	..	..	0°528	
	19. vi	113	..	..	..	..	12	51	50	..	..	..	0°519	
	26. vi	72	..	..	..	..	5	33	34	..	..	..	0°521	
	3. vii	82	..	..	..	..	7	41	34	..	..	..	0°518	
	10. vii	98	..	..	..	..	30	42	26	..	..	..	0°501	
	17. vii	94	..	..	..	..	42	42	10	..	..	..	0°494	
	24. vii	101	..	..	..	..	44	48	2	..	..	..	0°487	
	31. vii	108	..	..	..	..	7	53	49	4	..	..	0°487	
	7. viii	75	..	..	..	..	6	42	27	..	..	..	0°474	
	14. viii	68	..	..	..	..	8	35	25	..	..	..	0°479	
	21. viii	107	..	..	..	..	6	47	52	2	..	..	0°488	
	28. viii	64	..	..	..	..	11	24	29	..	..	..	0°481	
	11. ix	60	..	..	..	..	7	27	26	..	..	..	0°480	
	2. x	78	..	..	..	..	10	40	26	2	..	..	0°473	
	IV	17. i	28	..	I	13	14	..	..	..	..	..	..	0°419
		23. i	21	..	..	8	12	I	..	..	..	..	..	0°424
30. i		15	..	..	3	10	2	..	..	..	..	..	0°435	
6. ii		10	..	..	4	4	2	..	..	..	..	..	0°427	
13. ii		8	..	..	I	4	3	..	..	..	..	..	..	
20. ii		68	..	..	4	43	21	..	..	..	..	..	0°441	
27. ii		67	..	..	2	49	16	..	..	..	..	..	0°441	
7. iii		67	..	..	I	38	28	..	..	..	..	..	0°449	
13. iii		36	..	..	I	24	11	..	..	..	..	..	0°446	
20. iii		56	..	..	2	16	37	I	..	..	..	..	0°461	
27. iii		11	..	..	..	5	..	..	..	..	..	..	0°452	
4. iv		27	..	..	..	I	22	4	..	..	..	..	0°474	
10. iv		57	..	..	..	3	44	10	..	..	..	..	0°476	
17. iv		77	..	..	..	3	66	8	..	..	..	..	0°474	
24. iv		54	..	..	..	17	35	2	..	..	..	..	0°462	
1. v		89	..	..	..	38	51	..	..	..	..	..	0°456	
8. v		68	..	..	6	43	19	..	..	..	..	..	0°444	
15. v		72	..	..	15	47	10	..	..	..	..	..	0°435	
22. v		84	..	..	10	49	25	..	..	..	..	..	0°443	
29. v		79	..	..	..	29	50	..	..	..	..	..	0°458	
5. vi		73	..	..	..	31	42	..	..	..	..	..	0°455	
12. vi		62	..	..	..	26	36	..	..	..	..	..	0°456	
19. vi		72	..	..	..	51	21	..	..	..	..	..	0°445	
26. vi		81	..	..	5	54	22	..	..	..	..	..	0°443	
3. vii		70	..	..	6	46	18	..	..	..	..	..	0°443	
10. vii		81	..	..	2	50	29	..	..	..	..	..	0°446	
17. vii		74	..	..	10	54	10	..	..	..	..	..	0°435	
24. vii		57	..	..	30	27	..	..	..	..	..	..	0°417	
31. vii		66	..	I	21	42	2	..	..	..	..	..	0°429	
7. viii		49	..	..	19	30	..	..	..	..	..	..	0°425	
14. viii		75	..	..	27	47	I	..	..	..	..	..	0°425	
21. viii		82	..	..	28	51	3	..	..	..	..	..	0°425	
28. viii		88	..	I	46	40	I	..	..	..	..	..	0°416	
11. ix		61	..	..	33	27	I	..	..	..	..	..	0°416	
2. x		77	..	..	25	50	2	..	..	..	..	..	0°427	
III		17. i	19	I	16	2	..	..	..	..	..	..	..	0°371
		30. i	16	I	13	2	..	..	..	..	..	..	..	0°369
		6. ii	13	I	11	I	..	..	..	..	..	..	..	0°373
		20. ii	53	..	19	34	..	..	..	..	..	..	..	0°388
	27. ii	32	2	19	11	..	..	..	..	..	..	..	0°378	
	7. iii	58	..	24	34	..	..	..	..	..	..	..	0°386	
	13. iii	44	..	5	38	I	..	..	..	..	..	..	0°397	
	20. iii	56	..	3	47	6	..	..	..	..	..	..	0°405	
	27. iii	9	..	..	8	I	..	..	..	..	..	..	0°404	
	4. iv	64	..	..	48	16	..	..	..	..	..	..	0°410	
	10. iv	55	..	..	35	20	..	..	..	..	..	..	0°413	
	17. iv	45	..	..	26	19	..	..	..	..	..	..	0°415	
	24. iv	36	..	4	29	3	..	..	..	..	..	..	0°403	
	1. v	65	..	5	59	I	..	..	..	..	..	..	0°398	
	8. v	73	..	21	52	..	..	..	..	..	..	..	0°390	
	15. v	65	..	45	20	..	..	..	..	..	..	..	0°376	
	22. v	36	..	8	28	..	..	..	..	..	..	..	0°391	
	29. v	104	..	2	85	17	..	..	..	..	..	..	0°408	
	5. vi	88	..	3	78	7	..	..	..	..	..	..	0°404	
	12. vi	63	..	6	56	I	..	..	..	..	..	..	0°395	
	19. vi	75	..	21	53	I	..	..	..	..	..	..	0°392	
	26. vi	86	..	28	58	..	..	..	..	..	..	..	0°389	
	3. vii	57	..	11	46	..	..	..	..	..	..	..	0°392	
	10. vii	71	..	14	57	..	..	..	..	..	..	..	0°392	
	17. vii	66	..	29	37	..	..	..	..	..	..	..	0°385	
	24. vii	87	I	61	25	..	..	..	..	..	..	..	0°377	
	31. vii	64	..	33	31	..	..	..	..	..	..	..	0°382	
	7. viii	65	..	54	11	..	..	..	..	..	..	..	0°373	
	14. viii	59	I	41	17	..	..	..	..	..	..	..	0°375	
	21. viii	68	..	50	18	..	..	..	..	..	..	..	0°376	
28. viii	54	I	47	6	..	..	..	..	..	..	..	0°369		
11. ix	52	2	48	2	..	..	..	..	..	..	..	0°365		
2. x	50	3	34	13	..	..	..	..	..	..	..	0°373		

THE THIXOTROPY AND DILATANCY OF A MARINE SOIL

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From the Department of Zoology, Queen Mary College, London

(Text-figs. 1-6)

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INTRODUCTION AND HISTORICAL

In a previous paper (Chapman & Newell, 1947) attention was called to the importance to their inhabitants of the thixotropic* and dilatant properties of marine soils. It will be recalled that the property of dilatancy, shown by the whitening of wet sand under the footstep, was first described by Osborne Reynolds (1885), and has subsequently been investigated chiefly by Freundlich and his collaborators (Freundlich, 1935; Freundlich & Jones, 1936; Freundlich & Röder, 1938). Reynolds considered that the close packing of particles in a liquid medium was altered by an applied force so that the interstitial volume was increased and more liquid was drawn from the periphery into the dilatant mixture. By these changes the dilatant mass becomes harder and more resistant to shear. Freundlich & Röder described the relation between thixotropy and dilatancy. They considered that thixotropy could be described as a reduction in resistance with increased rate of shear as opposed to dilatancy, in which increased shearing force brings about an increased resistance. Thixo-

* The term *thixotropy* was originally used by Peterfi and Freundlich for the isothermal reversible sol-gel transformation shown by some colloidal solutions, but it has now come to be applied more generally and is used to denote a system which shows a decrease in viscosity upon agitation or a decreased resistance to shear when the rate of shear increases. For example, a suspension of fullers' earth in water liquefies on being shaken or on being stirred, but sets in a few seconds when the agitation stops. Many paints are thixotropic and flow easily and smoothly when they are being applied (whilst they are subject to shearing forces) but their viscosity increases enough when brushing stops for them not to 'run'. Some interesting aspects of the subject are dealt with in articles by Pryce-Jones (1946) and Boswell (1948).

tropic properties are shown by a variety of substances among which are clays whose particles are anisotropic, being rod-like or plate-like in shape. The range of concentration of solid particles to liquid is also important in influencing the behaviour of the suspension to shearing forces, and in their work on quartz particles ($1-5\mu$ in diameter) in water Freundlich & Röder stated that dilatancy occurred only in the range 42-45 % by volume of the solid. Below 42 % the mixture remained fluid however rapidly it was stirred, whereas above 45 % it remained compact. They described a dilatancy viscometer for use with solid suspensions by means of which they investigated the thixotropic and dilatant properties of a number of mixtures. It was admitted, however, that the machine was difficult to use with suspensions of particles above 50μ (0.05 mm.) in diameter. The dilatancy viscometer was described in detail by Röder (1939) in a paper in which is also set out the relation between particles and dispersion medium. Röder's apparatus and results have been criticized on technical grounds by Van Selms & Kruyt (1943), and another machine for the measurement of the consistency of plastic suspensions has been described by them in their investigation of the effect of a third phase on the rheology of suspensions of quartz particles and glass spheres in carbon tetrachloride (Kruyt & Van Selms, 1943*a, b*). It is not suitable for use with marine soils.

Freundlich & Juliusburger (1935) described an investigation into the thixotropy of quicksands and came to the conclusion that, whereas some quicksands have a larger clay content than neighbouring ordinary sands, this cannot be taken as a generalization and that other factors must be taken into account.

The soil of the Whitstable Flats. Clays, in general, are notably thixotropic, and it may be that even a small amount of clay is sufficient to alter the properties of suspensions of particles of larger size. Sand from the Flats at Whitstable in which *Arenicola marina* is so abundant can be said to possess quicksand or thixotropic properties, although to a much lesser extent than those soils which are recognized as true quicksands. The soil of the Flats is reasonably uniform for a distance of about 400 yd. between tidemarks and is characterized by having a sandy-coloured upper layer of about 1 in. in depth and a deeper layer of 6-12 in. in depth, black in colour but similar in particle-size composition. On exposure to the air this black sand becomes identical in appearance with that of the uppermost layer, the two layers being similar in all features except in the chemical composition of the iron compounds which they contain. A preliminary investigation showed that the soil consists largely of 'fine sand', as defined by Robinson (1932), of particle size between 0.2 and 0.02 mm. diameter with an admixture of 1-3 % of 'silt and clay' of particle size less than 0.02 mm. diameter. Eighty per cent. of the sand passes a 100-mesh sieve and therefore has a particle diameter of less than 0.12 mm. which, although above the upper limit of 0.05 mm. diameter given by Freundlich & Röder as suitable for use in the dilatancy viscometer, is not so widely dif-

ferent from their figure as to suggest that useful results might not be obtained by the use of their machine.

The interest in the present inquiry lies in the relation of the physical properties of marine soils to the habits of the animals which inhabit them. Some of the properties which appear to be of importance and which have been studied are the resistance to penetration, the thixotropic properties and their variations with changes of composition of the soil.

I am grateful for help at various times to Professor P. G. H. Boswell, F.R.S., Professor A. J. Grove, Dr G. E. Newell and Dr G. W. Scott-Blair.

THE MEASUREMENT OF RESISTANCE TO PENETRATION

For the easy testing of marine soils *in situ* the apparatus described by Chapman & Newell (1947) was used. This penetrometer was modified by the provision of a scale by which readings in the field were made easier to take. A diagram of the modified instrument is given in Fig. 1, from which it can be seen that when the slider or collar (C) is held in the hand, and the disk (D) placed upon the sand, pressures varying from zero upwards can be obtained. By calibrating the penetrometer against weights counterpoised on a balance the thrust exerted on the sand by the disk can be measured. A series of springs of different gauge steel wire give the instrument a considerable range. A graph of weight counterpoised against scale reading was made for each spring. This rather crude method of calibration had the advantage that the instrument was manipulated in the way in which it was used in the field when measurements were being made.

In use the instrument was held as nearly vertical as possible and was pressed gently into the soil, the reading on the scale being then noted. Ten or more readings were always made and a mean calculated, the pressure equivalent to the scale reading being then read off from the graph. The hardness of the soil is here expressed as grams per square centimetre necessary for penetration. It was fairly easy, with practice, to obtain a 'good' or close set of figures for any particular locality, but in order to do so it was necessary on occasions to discard readings, for example, when it was clear that the penetrating disk had struck a larger stone or had penetrated a worm burrow.

The measurements made with the penetrometer are correlated in this paper with other features of the soil such as water content or the burrowing speed of *Arenicola*. Accordingly, the results are set out in conjunction with details of the features with which a connexion was being sought and the results of the tests (expressed always as g./cm.² necessary for the penetration of a disk of area 0.125 cm.² to a depth of 3 cm.) will be found in the section dealing with the burrowing speed of the lugworm (p. 136). But, to anticipate briefly, both the hardness of the soil and the time taken by the lugworms to burrow was found to increase as the water content decreased.

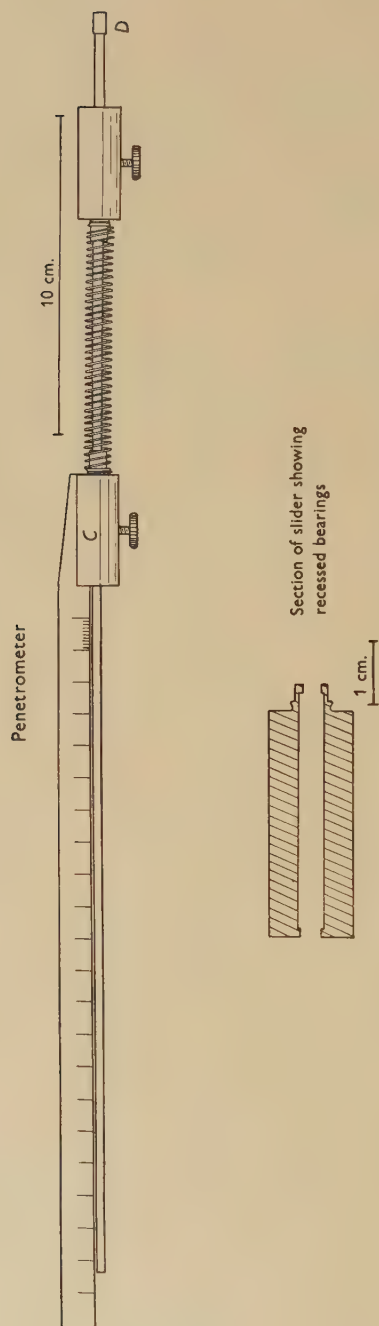


Fig. 1. The modified penetrometer. *C*, slider or collar. *D*, penetrating disk.

THE THIXOTROPY AND DILATANCY OF MUDDY SAND

One striking feature of the soil of the Flats is the difference between its physical properties when wet and when dry. For example, if water is slowly added to a sample of dry sand it becomes a darker brown as it is wetted. It is hard when touched with a glass rod. Small portions, made up of adhering particles, can be broken off. It does not appear to flow when it is tapped. In fact, it behaves almost as a friable solid.

As more water is added the material 'settles' when the vessel containing it is agitated so that it has a level, shiny but not plane, surface. There is, therefore, sufficient water to appear at the interstices of the superficial particles. When the mass is prodded with a glass rod the colour becomes lighter and the appearance no longer shiny but dull or matt. Its resistance to penetration increases as the rod is pushed in.

The addition of still more water causes the surface to become plane; there is a layer of water unbroken by particles. No lightening of the colour occurs when the mass is prodded nor does the surface become matt in appearance. Its resistance to prodding is smaller and does not increase as distortion occurs.

In other words, the mixture of sand and water apparently shows a variety of properties ranging from those of a dilatant to those of a thixotropic material, according to the proportions in which the sand and water are mixed.

An attempt was therefore made to obtain some more exact measurements of the thixotropic and dilatant properties of the sand and to correlate these with the mechanical analysis and water content. Tests were made in the dilatancy viscometer of Freundlich & Röder which is described below. Before being used the sand was passed through a 2 mm. round-holed sieve to remove any large particles such as shells which are found in the soil but which are not invariable constituents.

Apparatus

No detailed description of their dilatancy viscometer was given by Freundlich & Röder, but it was described in detail by Röder (1939). A piece of apparatus was made which appeared to embody the essential features of the machine described. It is a device (Fig. 2) for pulling a sphere through the substance to be investigated. The soil is contained in a brass trough of square section 1.6 cm. deep and 50 cm. long. Above the trough are arranged two brass guide rails, one vertically above the other, between which runs a small carriage. Fixed to this is a narrow shaft ending in a phosphor-bronze sphere of diameter 5 mm. which can thereby travel along the locus of the long axis of the trough. The construction of the carriage is also shown in Fig. 2. It is attached by a thread, running over a pulley at one end of the guide rails, to a pan for holding weights. The pulley, carriage wheels and guide rails are of

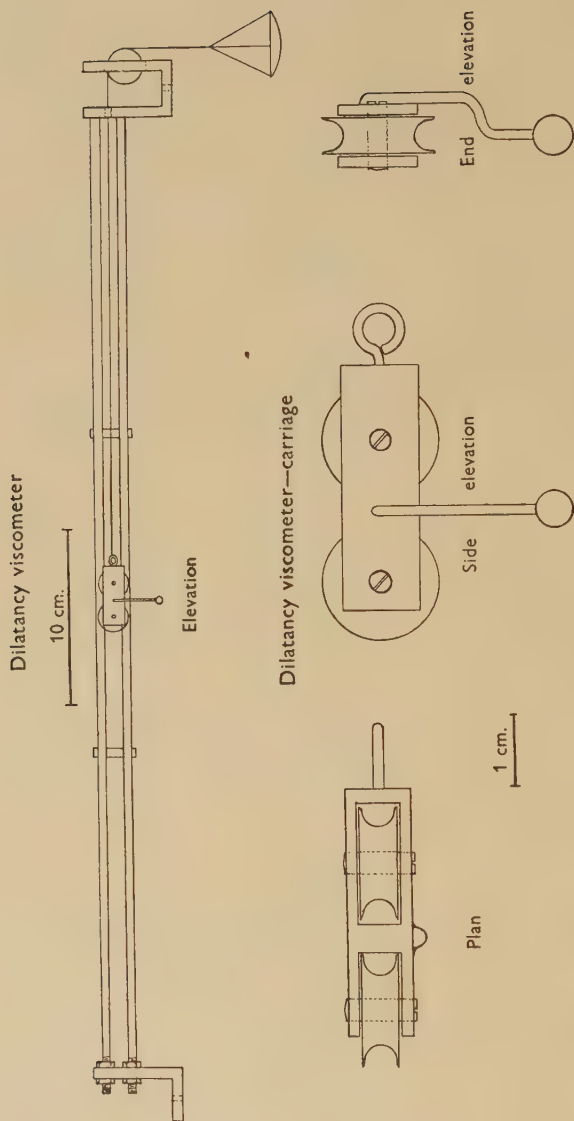


Fig. 2.

a high finish and are polished each time before use with household metal polish.

The time taken for the sphere to travel through a distance of 30 cm. was measured by a stop-watch to the nearest $\frac{1}{10}$ th sec. Prior to making each run the soil was treated in a standard way, being tapped forty times on the bench and being left for 60 sec. before the test was begun. Even after using this standard preliminary treatment it was difficult to ensure that the soil was always in a 'natural' packing similar to that found in the sand of the undisturbed shore.

Results

The results obtained with this machine were plotted graphically as speed (ordinate) against weights placed in the pan. Ignoring the friction forces in the apparatus, the curve given by a Newtonian liquid (glycerol) is a straight line passing through the origin. According to Freundlich & Röder a thixotropic substance also gives a straight-line graph, but instead of passing through the origin it cuts the abscissa some distance to the right. They obtained this result using a suspension of quartz particles in carbon tetrachloride, a non-polar liquid, instead of water in which their quartz was dilatant. When once movement of the sphere begins in a thixotropic system its speed is proportional to weight as for a Newtonian liquid, but a minimum force is necessary before movement can begin, whereas with a perfect liquid the smallest applied force causes movement. (It would appear, however, that this 'ideal' curve for a thixotropic substance is not fully in accordance with the definition of thixotropy as decreased resistance to increased rate of shear.) Freundlich and Röder point out that dilatant substances do not give a straight-line graph but one which is a straight line only over the first part of the range of applied weights. Above a certain weight it flattens out so that no further increase in weight gives any increase in speed. In other words, when slow movement is taking place in dilatant systems—with small applied weights—their behaviour is nearly that of Newtonian liquids, but at a certain speed no further increase is possible without an incommensurate increase in applied weight. The form of the curves as they should appear according to Freundlich & Röder is shown in Fig. 3. 'A horizontal part of the curve,' they say, 'implying solid behaviour, occurs in thixotropic systems at zero rate of shear, i.e. at rest.... Liquid behaviour is represented in both cases by a steep part of the curve; in thixotropic systems at a sufficiently high rate of shear..., in dilatant systems at rest and at small rates of shear.'

Preliminary tests showed that the behaviour of the soil was complex. For example, in a mixture of sand and water with a small amount of superfluous water on top and with a weight of 20 g. applied to the sphere, its speed through the soil was 0.05 cm./sec. on the first test after the trough was filled. After giving the trough forty taps and allowing the contents to settle for 60 sec., the speed rose to 3.0 cm./sec. After prodding the soil, as well as tapping it, the

speed fell to 0.3 cm./sec., whereas on the fourth test, preceded only by the standard tapping procedure, the speed had risen to 0.6 cm./sec. Further tests along these lines confirmed these results which showed that it was essential for the soil to be treated in a standard way before each test because the 'particle structure' of the soil was altered by the passage of the sphere, the alteration being at a maximum in rather dry sand, in which a clear channel was left. With dry sand the channel did not disappear even after the standard tapping procedure. The results of some of the preliminary tests, using sand saturated with sea water, are shown graphically in Fig. 4. It will be seen that there is no hint of a break in the curve such as Freundlich & Röder say occurs with a dilatant material.

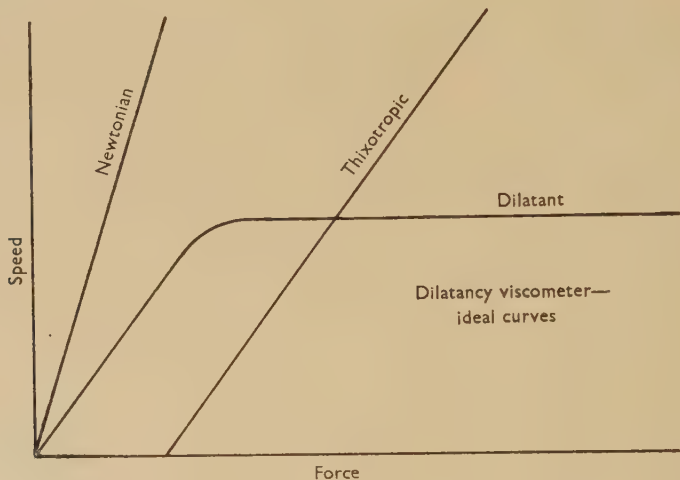


Fig. 3. Graph showing 'ideal' curves obtained by the use of the dilatancy viscometer.

The standard tapping procedure adopted may depend for its efficacy in standardizing the structure of the soil on the property described by Freundlich & Jones as *rheopexy*. Suspensions showing this property solidify more quickly when subjected to moderate agitation.

The effect of variations of water content

If the soil behaved as a thixotropic substance when excess of water was present, might it not become dilatant when the water content was reduced? In order to test this possibility runs were made in the dilatancy viscometer using soil containing a different amount of water. The samples of sand and water were prepared by filling the trough with damp soil and adding sufficient water to cover it completely. Water was then drained off until the appearance of the soil was considered suitable. After the tests had been made the soil was scraped into a weighed beaker and dried in an oven at 105° C. until of constant weight.

from these weighings the water content was calculated. The results are given in Table I and are also shown plotted graphically in Fig. 5.

As can be seen from the table the results are not clear-cut. It is apparently true to say that the speed of the sphere is greater when the water content is

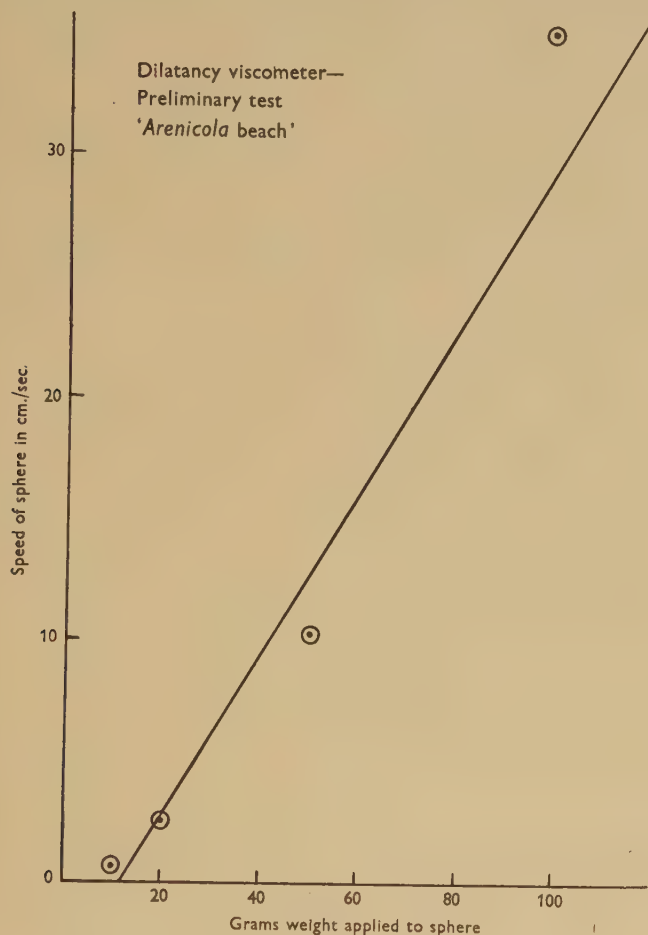


Fig. 4. Preliminary results of dilatancy viscometer tests.

higher, but over the range of weights applied the effects of dilatancy do not appear in the graphical result. The results agree with a thixotropic behaviour of the substratum in that the graphs cut the abscissa to the right of the origin. Against that, however, must be set the appearance of the sand. Especially when its water content is low its appearance is clearly of the dilatant type whilst the sphere is travelling through it. In front of the sphere the surface layer of the soil is shiny but not plane, the water surface being broken by sand

TABLE I. THE EFFECT OF WATER CONTENT ON THE SPEED OF A SPHERE PASSING THROUGH MUDDY SAND FROM THE *ARENICOLA* REGION OF THE WHITSTABLE FLATS

Speed of sphere in cm./sec. Water content expressed as percentage wet weight of mixture. Almost all the figures for the speed of the sphere represent a mean of not less than three readings.

Wt. applied to sphere (g.)	Soil saturated	Soil with 28 % water	Soil with 21 % water
9	0.16	—	—
10	—	—	0.04
11	0.4	—	—
15	0.9	—	—
20	0.9	0.25	0.15
30	1.5	—	—
40	—	0.9	—
50	3.8	2.7	1.25
100	8.6	6.0	3.8

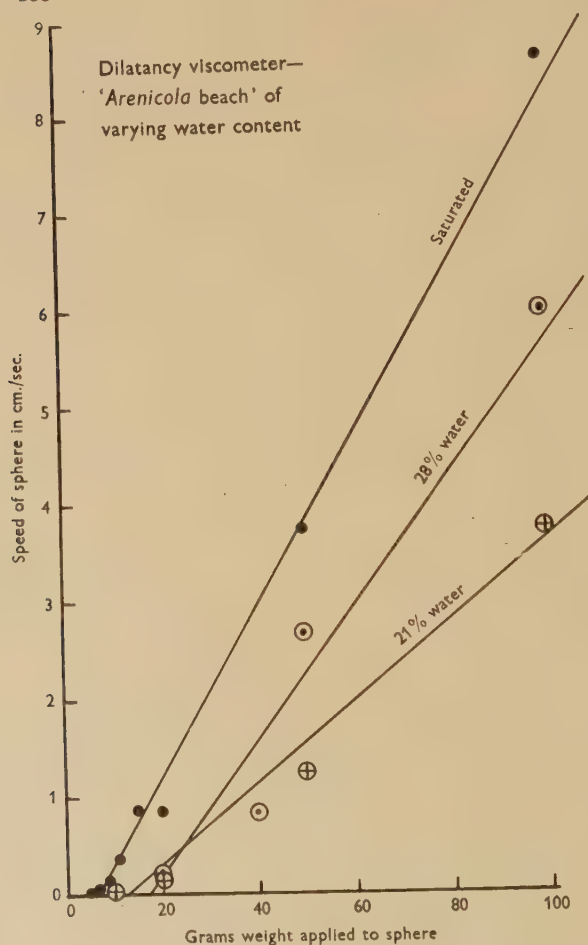


Fig. 5. Results of dilatancy viscometer tests on sand with varying water content.

particles. Alongside and behind the sphere the surface appears dull or matt, the water now being insufficient to fill the enlarged interstices. This behaviour is characteristic of dilatant substances, as is the behaviour of the sand when the trough is being emptied. The sand becomes quite hard and firm so that it cannot be induced to flow but has to be scraped out.

It appears then as if the sand exhibits both dilatant and thixotropic properties in one sample and that, although its pore space may increase with the application of an external force, the resistance to shear does not reach a maximum at any particular rate of shear tested. It is possible, but unlikely, that this phenomenon was not shown over the range of forces which were applied. It is also possible that the amount of silt and clay present in the mixture was sufficient to render the mutual slipping of the particles easy enough to avoid any great increase in resistance to the applied shear force while yet not completely masking the fact that increase in pore space *is* effected by the shear force.

The effect of the removal of silt and clay

To see if a small amount of silt and clay might affect the physical properties of the soil, tests were made with the dilatancy viscometer, using sand which had been repeatedly washed in such a way that all the silt and clay were removed and all the fine sand left. This was done, as in the estimation of the various soil fractions by the method of Robinson, by the decantation of the supernatant liquid to a depth of 10 cm. at a time of 4 min. 48 sec. after the sample was dispersed by agitation. After repeated washings the sea water no longer appeared turbid and it was clear that all the silt and clay had been removed, unless there was any still adhering to the sand particles which could not be removed by washing but which might yet affect the physical properties.

Two tests were made with the washed sand, one in which there was a superfluity of water and the other in which the water content was found by subsequent analysis to be 21 % by weight. The results are given in Table II and are plotted graphically in Fig. 6.

There was no very noticeable difference in behaviour between the washed and the unwashed sand during the course of the tests, and this was borne out by the graph which again showed that there was no clear indication, by a break in the straight line, of any marked dilatant behaviour of the sample of soil.

Discussion

Indeed, as Freundlich & Röder remarked, the dilatancy viscometer is difficult to use with large particle systems, and it may be that therein lies the reason for the absence of any clear sign of dilatancy in the numerical results in spite of the clear signs of dilatancy given by qualitative tests. The only thing that does emerge clearly is that it takes longer for the ball to travel through drier sand than through wetter sand under a given weight, and that this is

TABLE II. THE EFFECT OF WATER CONTENT ON THE SPEED OF A SPHERE PASSING THROUGH WASHED, SILT-FREE SAND FROM THE *ARENICOLA* REGION OF THE WHITSTABLE FLATS

Wt. applied to sphere (g.)	Soil saturated	Soil with 21 % water
10	0.3	—
20	1.0	—
30	1.8	—
40	2.5	—
50	3.5	< 0.2
100	7.5	< 0.3
200	20.0	0.7

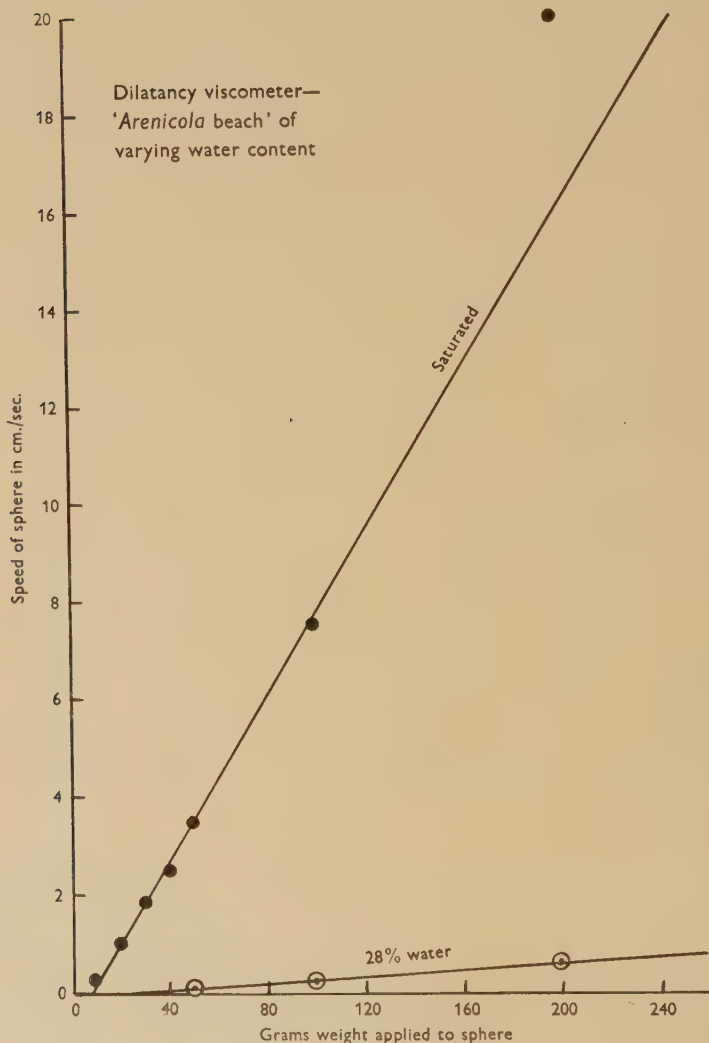


Fig. 6. Results of dilatancy viscometer tests with washed sand

supported by the hardness measurements made with the penetrometer. Clearly the water content is important in the determination of the resistance of the sand to gross penetration and equally clearly the presence of excess water is necessary for the sand to become almost fluid as it may do when agitated. What is suggested, perhaps, by the straight-line graph of speed against force (which is characteristic of Newtonian liquids as well as of thixotropic substances) is that the limiting factor in the passage of the sphere through the system is the viscosity of the water. It can easily be seen in suspensions with only a small quantity of superfluous water above the sand that there is a visible flow of liquid from in front of to behind the sphere as it passes through the mass. If it can be shown that the sphere in its passage through the suspension leaves behind it a clear, fluid-filled channel (as it can be seen to do in relatively dry suspensions), then the liquid filling the channel has had to flow into its new position from elsewhere in the suspension. Clearly then, if there is a superfluity of liquid, more than enough completely to fill the interstices between the particles, liquid can flow in from all directions and will not have to come from very far away from the point at which the clear channel is being made. If, on the other hand, there is not a great superfluity of water, liquid will have to come from a greater distance away in order to fill the channel which is being made. Since it comes from a greater distance the time taken for it to accumulate will be greater and hence the speed of the sphere through the suspension slower.

If these suggestions are correct, then they would account for the straight-line graph obtained, because the relations of speed and force depend on the viscosity and density of the water which is a Newtonian liquid. Owing to turbulence of flow through the interstices between the particles the effect of viscosity is partly lost. But the hypothesis can be roughly checked by the substitution for water of other liquids with higher or lower viscosities and densities, the substitution of liquids with a higher viscosity and density should result in a slower rate of travel, and of liquids with a lower viscosity and density in a greater rate of travel for the same applied force.

Tests were accordingly made with dry sand to which was added one of the three polar liquids glycerol, water and ether, the viscosities of which are in the approximate ratio of 5000:5:1 and the densities in the approximate ratio of 1.6:1.3:1. With the same weight in the scale-pan the speed of the sphere through sand-glycerol, sand-water and sand-ether mixtures was in the approximate ratio of 50:5:1. Had the viscosity factor alone been operative the ratio of speeds should have approached more nearly to 5000:5:1, and had the density factor alone been operative the ratio of speeds should have been nearer to 1.6:1.3:1. In a general way the results of this test confirm the suggestion that the viscosity and density of the interstitial liquid may be one of the main factors influencing the movement of marine soil. It is not suggested that this has been proved but merely that the absence of any kind of dilatant behaviour

revealed by the viscometer and the rough correspondence of speeds and viscosities and densities suggests that the physical properties of the liquid determine the behaviour of marine soils *as well as* the size of the component particles.

SOIL HARDNESS AND BURROWING SPEED OF *ARENICOLA*

Since the purely physical method of the dilatancy viscometer did not show clearly any very striking difference between washed and unwashed sand, or between saturated and drier sand, a biological method was tried for testing the properties of the soil. The speed of burrowing of *Arenicola marina* L. was used for this purpose, since a certain amount is already known about this activity (Chapman & Newell, 1947). The usefulness of the animal as a biological tool is due to the fixity of its behaviour. When placed upon the surface of the substratum it at once begins to burrow in, whether its ventral or its dorsal surface is in contact with the soil. It seldom attempts to 'right itself' first. If the first attempt with its proboscis should fail to find a suitable spot it may try other places, but equally, it may persist for some time in attempting to force its way into an unsuitable place. Its behaviour seems quite unchanging although the environment may vary. This fixity does not leave scope for any kind of crawling or seeking behaviour. Hence, when the creature is placed on a soil into which it is not prevented from burrowing by large stones, the time which it takes to enter the soil, from the instant at which it is placed on the surface, can be taken as an indication of the difficulty which it has in the penetration of the soil.

The time taken by samples of worms to burrow into sands of different water content was measured and the sands subsequently sampled and analysed. The sampling was done with a cork borer which removed, with very little disturbance, a cylinder of soil of 1 cm. diameter; the analysis was done by drying a sample of some 15 g. to constant weight at 105° C. The samples of sand of different water content, in which the exercises were carried out, were arranged by making small mounds of different heights on the Flats. Water then drained from the upper parts of these leaving them drier than the surrounding shore. Alternatively, a circular moat was dug round a central 'island' which again became drier by the draining of water into the moat. This latter method had the advantage of not disturbing the natural structure of the sand. But even in the other method an attempt was made to preserve this structure as far as possible by being careful to construct the mound of clean spits of sand, in which the natural upper surface was left uppermost.

In the first set of experiments three batches, each of ten worms, were used. The first batch constituted a control and were allowed to burrow into undisturbed sand, the second batch were set to burrow into a low mound and the third batch into a higher mound. In the first set of experiments the water

content of the mounds was not estimated. A second set of experiments was made in a similar fashion and the water content of the soil was estimated. A selection of the detailed results of these tests is set out in Table III. They are quite clear-cut and from them it can be seen that the worms were quite unable to burrow into the high mound from which the water appeared to have drained. Some of them could burrow into the low mound, but those which succeeded in doing this took longer than the worms which burrowed into the undisturbed sand. Worms which had been trying to burrow into the high mound were put on to the surface of undisturbed beach, into which they burrowed at about the normal rate.

Although the weighing error in estimating the water content of the sand samples did not exceed $\pm 0.1\%$ it would seem that the accuracy of sampling, even if not the accuracy of estimation of the water content, was not sufficiently accurate to yield useful results. It may be that the method of taking the sample, disturbing the sand as little as it did, was yet unsuitable for the estimation of very small differences in the water content. It was, however, very striking that the animal was quite unable to cope with the drier sand which, of course, was distinctly harder to feel and apparently dilatant when disturbed. It would appear that another method of estimating the effect which diminution of its water content had on the sand was necessary, so that hardness tests were made with the penetrometer.

TABLE III. THE EFFECT OF THE WATER CONTENT OF THE SAND ON THE BURROWING SPEED OF *ARENICOLA*

Worm no.	Time to burrow to end of branchial region in min.		
	Control, undisturbed sand	Mound of height 10 cm.	Mound of height 25 cm.
1	2.25	2.75	Unsuccessful
2	2.5	4.0	..
3	3.0	5.25	..
4	3.5	5.5	..
5	3.5	10.0	..
6	4.0	Unsuccessful	..
7	4.0	..	..
8	4.5	..	..
9	Damaged	..	..
10	..	..	..

After 10 min. the worms from the high mound were placed on undisturbed sand when they burrowed in the following times: 2.5, 2.75, 3.5, 4.0, 4.25, 4.5, 5.0, 5.25, 5.5, 5.75.

In the third set of experiments the same methods as before were used to produce small areas of soil in which the water content differed from that of the surrounding shore, but the water content of the soil was not estimated. Instead the hardness of the soil was measured with the penetrometer. The results are given in Table IV from which it can be seen that they agree with the first two sets of tests. As the height of the mound increases so the

hardness of the soil increases and the ability of the worms to burrow into it decreases.

A synopsis of the experiments on the correlation of soil hardness and burrowing times is set out in Table V.

CONCLUSIONS

The aim of the work which has been set out in this paper is ultimately to determine to what extent the physical properties of the substratum determine the kind and number of its inhabitants, particularly in the intertidal zone. It is well known that some worms prefer fine soil, others a coarser medium, but it

TABLE IV. THE EFFECT OF WATER CONTENT ON THE HARDNESS OF THE SOIL AND THE BURROWING SPEED OF *ARENICOLA*

Burrows made into mounds of varying height above water level. Time to burrow in min. and sec. Hardness in g./cm.² required for penetration. (Each figure represents a mean of not less than twelve readings.)

Worm no.	Mound height zero. Hardness	Mound height 5 cm. Hardness	Mound height 7.5 cm. Hardness	Mound height 13 cm. Hardness
	1088	1616	1961	2272
1	2.30	4.20	8.00	6.00
2	3.15	4.35	16.00+	10.00
3	4.00	4.45	16.00+	10.00
4	4.10	4.50	16.00+	Unsuccessful
5	4.20	5.15	Unsuccessful	..
6	5.00	5.50	..	..
7	5.05	7.20	..	..
8	5.05	8.00	..	..
9	5.10	8.10	..	..
10	5.15	8.30	..	..

TABLE V. SYNOPSIS OF HARDNESS AND BURROWING EXPERIMENTS

Hardness of soil (g./cm. ²)	Burrowing time or percentage of animals burrowing	Height of mound (cm.)
1088	4.38 min.	Zero
1616	6.17 min.	5.0
1961	40 %	7.5
2272	30 %	13.0

is not known precisely how these changes in composition affect the properties of the soil which are important to the animals. In the intertidal zone, from which the soil used in the experiments was obtained, even an apparently uniform environment may be subject to small local variations of silt or water content which are sufficient to bring about marked changes in the properties of the soil. The Flats at Whitstable are uncovered for about 10 out of the 24 hr., so that the time during which the animals may be subjected to varying physical conditions is an appreciable part of their life. The slope of the shore, which is

here very gradual; the nature of the underlying stratum, whether porous or impervious; small local variations in elevation; shelter from wind or sea scour; all these may serve to alter the physical properties which have been studied.

An attempt has been made to show that the properties of thixotropy and dilatancy, which are of importance to burrowing animals, are affected by water content, that the hardness of the soil varies with water content and that the burrowing speed of lugworms is also affected. It is disappointing to find that the physical method of investigation using the dilatancy viscometer of Freundlich & Röder did not give clear-cut results, and did not show that there was any marked difference in properties between wet and dry sands, nor between those containing silt and clay and those which had been washed free from small particles. But the results obtained from the machine suggest that it is the density, viscosity and amount of water which determines to a large extent the fluidity of the sand on agitation. This conclusion was supported by tests which were made using liquids having viscosities and densities different from that of water.

Changes in the amount of water mixed with the sand of the Flats caused a marked change in its hardness and the speed with which lugworms could burrow into it. This is clearly a property which may be of great importance in the distribution of *Arenicola*. At Whitstable the sand is underlain by impervious clay and does not dry out at low water. It is possible that the worms can 'work' the headshafts of their burrows (Wells, 1945) at all states of the tide. But if there were no clay to retain the water, then at low tide the drained soil would become too hard for them to 'work', their feeding time would be limited to the time during which they were covered by the water and their distribution might well be limited also. The Flats appear too uniform in water content and worm population for the correlation of these features to be very striking, and it is hoped that some more suitable site will be investigated. But it is clear that there are considerable differences in the density of population of small local areas, the arrangement of the burrows in straight lines being one of the most striking (Newell & Chapman, 1948).

The effect of the clay content on the physical properties of the soil, for which it was not easy to obtain numerical data from the dilatancy viscometer, may also prove more susceptible of investigation by a biological method. The burrowing speed of *Arenicola* which has been correlated with the hardness of the soils would clearly be suitable for this purpose.

SUMMARY

Modifications are described to the penetrometer originally designed by Chapman & Newell (1947) for the measurement of the resistance to penetration of marine soils.

An account is given of qualitative and quantitative tests made during the study of the thixotropy and dilatancy of the muddy sand of the *Arenicola* region of the shore at Whitstable. The results of tests made with the dilatancy viscometer originally used by Freundlich & Röder are shown not to be in clear agreement with the observed behaviour of the soil.

It is suggested that the fluidity or otherwise of a marine soil is a function of the viscosity and density of the liquid filling the interstices between the particles.

It is shown that the resistance to penetration of the soil and the burrowing speed of *Arenicola* are dependent upon the water content.

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THE USE OF PROBABILITY PAPER FOR THE GRAPHICAL ANALYSIS OF POLYMODAL FREQUENCY DISTRIBUTIONS

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(Text-figs. 1-6)

The mathematical analysis of bimodal distributions is very complex. Karl Pearson (1894) investigated the problem and developed equations for the purpose; but found them unsolvable as the 'majority [of the relations] lead to exponential equations the solution of which seems more beyond the wit of man than that of a numerical equation even of the ninth order'. He did indeed evolve an equation of this order and used it to analyse a few bimodal distributions, but the arithmetic involved was very laborious. Later he (Pearson, 1914) gives a table for 'Constants of normal curve from moments of tail about stump' which, as he describes in the introduction, occasionally permits a rough analysis of a distribution which is known to be bimodal. This method is much more rapid than the solution of the nonic equation, but 'owing to the paucity of material in tails and corresponding irregularity there will be large probable errors'. Gottschalk (1948) discusses the question and shows that in the special case where the bimodal distribution is symmetrical comparatively simple solutions can be found.

The purpose of this paper is to describe by a series of examples a straightforward graphical method which enables one to analyse not only bimodal distributions, both symmetrical and asymmetrical; but also more complex distributions. The last example will show how a distribution comprising three unequal and overlapping populations can be analysed, an estimate being obtained of each separate mean, each separate standard distribution, and the relative proportions in which the three populations are mixed.

The method makes use of probability graph paper¹ devised by Hazen (1913) for the analysis of the flow of water in rivers. The use of this and other probability papers for various engineering and industrial purposes has been described by Rissik (1941), Doust & Josephs (1941-42), Levi (1946) and others; but I know of no description of its use for the analysis of bimodal or polymodal distributions. Perhaps the methods I am describing are so obvious to mathematicians familiar with probability graph paper, that for them description is superfluous. To the biologist, however, the simplicity of this

¹ Obtainable from Messrs Wightman Mountain, London, as 'Data sheet No. 37. Arithmetic Probability'. A similar paper is also stocked by H.M. Stationery Office.

powerful tool is perhaps its greatest attraction. He has long been aware that the mean and standard deviation of populations he is confronted with are often of little biological significance; because these populations are compounded of individuals belonging to the two sexes, to different species, or to different age-groups, and are therefore necessarily bimodal or polymodal in character.

Hazen's probability graph paper (Fig. 1) has along the bottom a scale of percentages reading from 0.01 % on the left to 99.99 % on the right (Fig. 4 shows the complete ruling). Along the top of the paper the same scale reads from right to left. The scales are not evenly spaced; but are much more crowded in the middle than at the sides, being specially arranged so that when any normally distributed population is plotted, in a manner which will shortly be described, the points all fall on a straight line. The position of this line is determined by the mean and its slope by the standard deviation, and these statistics may be estimated without laborious calculations. If a bimodal or polymodal distribution is compounded of distributions which are themselves normally distributed, and with biological data this is generally true enough for practical purposes, it will give a curve when plotted which is the resultant of two or more straight lines.¹ These lines are usually not difficult to find and the irrespective positions and slopes give the means and standard deviations of the component populations.

Fig. 1 shows the analysis of 1572 cuckoos' eggs each measured to the nearest half millimetre. The histogram to the left of the figure gives the size distribution; there are for example 156 eggs between 20.75 and 21.25 mm. in length. The histogram is not part of the method, but is included to facilitate description.

The data are plotted as cumulative percentages. Take, for example, the point *P* indicated by a small circle: here 4.7 % (scale along the bottom) of the sample is less than 20.75 mm. in length, for there are $1 + 3 + 30 + 39 = 73$ eggs or 4.7 % of 1572 eggs shorter than this. Alternatively, 95.3 % (scale along the top) of the sample of eggs exceed 20.75 mm. in length. When all the points are plotted it is found that they lie approximately in a straight line *AB*. This line represents a normal distribution whose mean length is the length corresponding to the point *M* at which the line cuts the vertical for 50 %. i.e. 22.35 mm. The standard deviation is estimated from the points *S*₁ and *S*₂ where the line *AB* cuts the verticals for 15.87 and 84.13 % respectively, *S*₁ corresponds to a length of 21.35 mm. and *S*₂ to 23.4 mm. and the standard deviation is half the difference $(23.4 - 21.35)/2 = 1.025$ mm. This is because 15.87 % of any normally distributed population is less than the mean by an amount equal to the standard deviation or more, and another 15.87 % exceeds the mean by this amount. The vertical lines for 15.87 and 84.13 % are no

¹ Apart from 'Normal' distributions the ones most frequently encountered with biological data are 'log-normal' and Poisson distributions. Log-normal distributions may be handled either by plotting the logarithm of the measurement instead of the actual measurement, or by the use of logarithmic probability paper, and Doust & Josephs (1941-42) describe a probability paper which is specially designed for Poisson distributions.

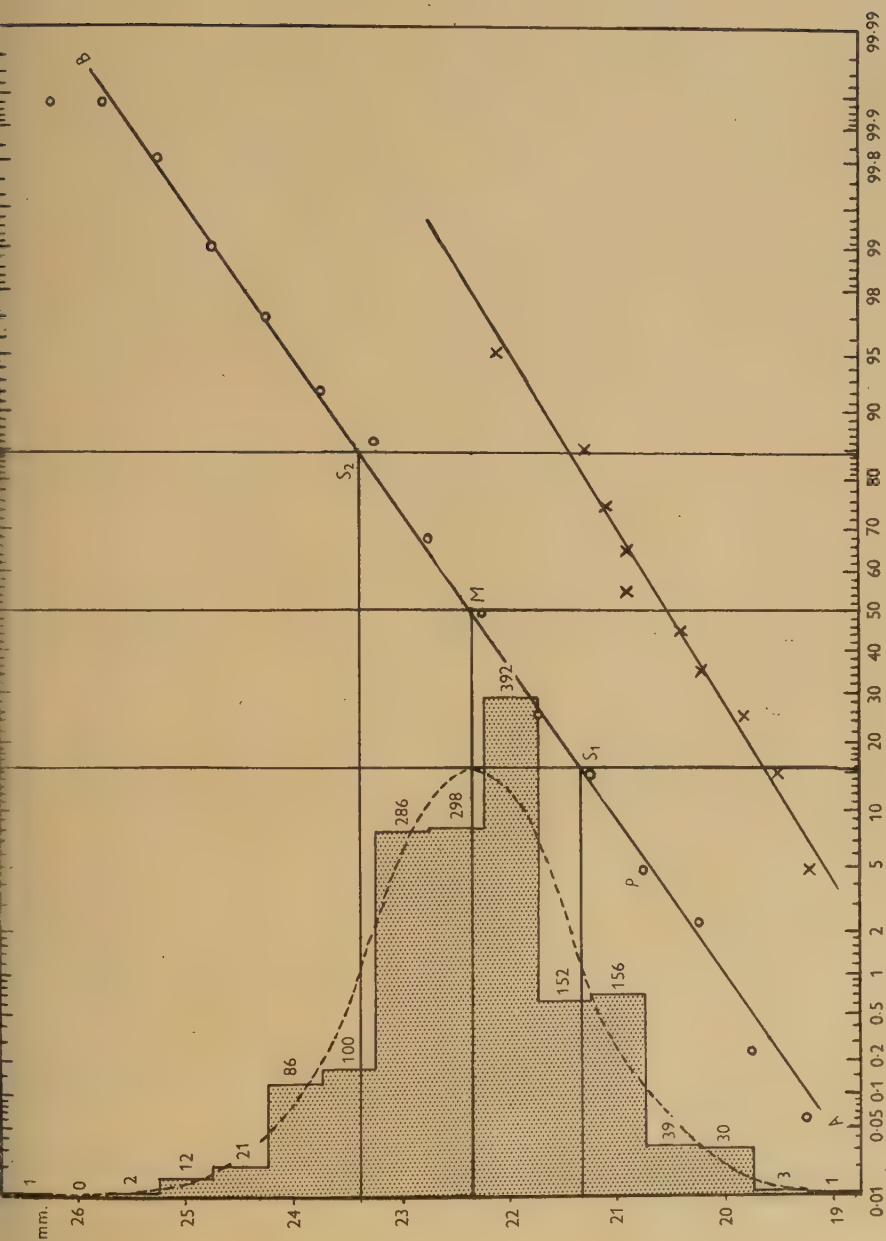


Fig. I.

marked on the paper as supplied; but are easily put in. A 10 in. slide-rule is sufficiently accurate for plotting results.

When the number of observations is less than about twenty-five an alternative method of plotting is appropriate, as a frequency tabulation is of little value with small samples and may lead to considerable grouping errors. The data are arranged in ascending order of magnitude, each individual observation is then plotted in such a way that there are equal percentage intervals between each observation. In general, if there are N observations, the first in the sequence is plotted on the 'probability' line whose value is $50/N\%$, and the succeeding $(N-1)$ observations at equal intervals of $100/N\%$. To give a concrete example, a sample of ten individuals gave the following measurements: 20.9, 20.4, 19.2, 21.1, 20.9, 22.1, 21.3, 19.8, 19.5, 20.2. These are arranged in ascending order and given the appropriate percentage value (Table I).

TABLE I

Sequence no.	Measurement	Percentage
1	19.2	5
2	19.5	15
3	19.8	25
4	20.2	35
5	20.4	45
6	20.9	55
7	20.9	65
8	21.1	75
9	21.3	85
10	22.1	95

The measurements are plotted against the percentages as indicated by the X 's in Fig. 1, and a straight line drawn through the points enables one to estimate the mean and the standard deviation as 20.5 and 0.9 mm. respectively. Neither method of plotting will give precisely the same estimates of the mean and standard deviation as the arithmetical method; but the graphical solution gives estimates of the true values for the population which are as reliable as any that can be obtained from the sample. If there is difficulty in placing a straight line through the points, it is at once apparent that the sample is an aberrant one; but there is nothing to indicate this with the usual arithmetic procedure.

In Fig. 2 the size distribution of forty-one immature copepods is analysed. These were all of the same species and all in the same developmental stage; both sexes were present, probably in approximately equal numbers, but it was impossible to tell the sex of any individual. The size distribution of the sample is shown by the histogram on the left. When plotted on the probability paper the points do not fall on a straight line but on a sigmoidal curve. The dotted line GLH was not drawn to fit the points plotted from the data, but is the resultant of the two straight lines CD and EF . The lines CD and EF were found by assuming that the distribution was a bimodal one due to the

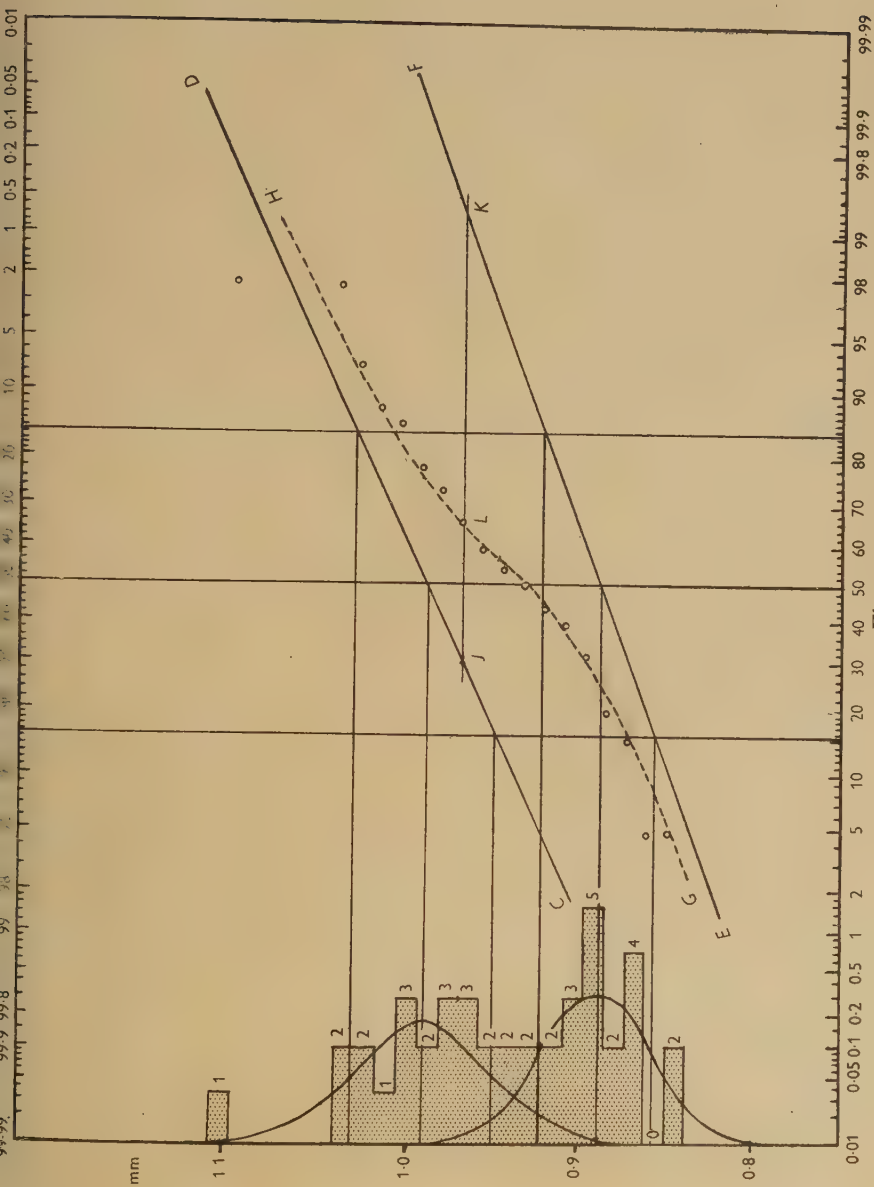


Fig. 2.

difference in the average lengths of the males and females. It is known that the adult females are distinctly larger than the adult males and it is reasonable to assume a similar sex difference in the immature specimens measured. It is likely, therefore, that the smallest individuals, say those less than 0.9 mm. long are all or nearly all males, and that those longer than about 1.0 mm. are nearly all females. On this hypothesis the eight male individuals less than 0.88 mm. long which comprise 19.5 % of the total population will comprise 39 % of the male population (assuming that males and females are present in equal numbers). Similarly, the six males less than 0.72 mm. long are estimated to be 29.3 % of the male population. A few points plotted in this way for the small individuals are found to fall on a straight line which is approximately that drawn, *EF*. Similarly, the doubling of the percentages for the largest size groups gives us a straight line *CD* or thereabouts. The resultant, *GLH*, of the two straight lines can now be drawn in. For example, the position *L*, where the resultant cuts the arbitrarily chosen horizontal line *JK*, is placed at 64.7 %; this being half the sum of the percentages for *J* and *K*, 30 and 99.4 % respectively. The precise position of the two lines should be adjusted by trial and error until positions are found whose resultant curve best fits the data. The means and standard deviations of the two populations can then be read off the scale. In the example, although only a small sample of forty-one individuals was available, and although no single individual could be sexed we are able to say, with a fair degree of confidence, that the average length of the males is about 0.885 mm. and that of the females about 0.99 mm. and that the standard deviations are of the order of 0.375 mm.

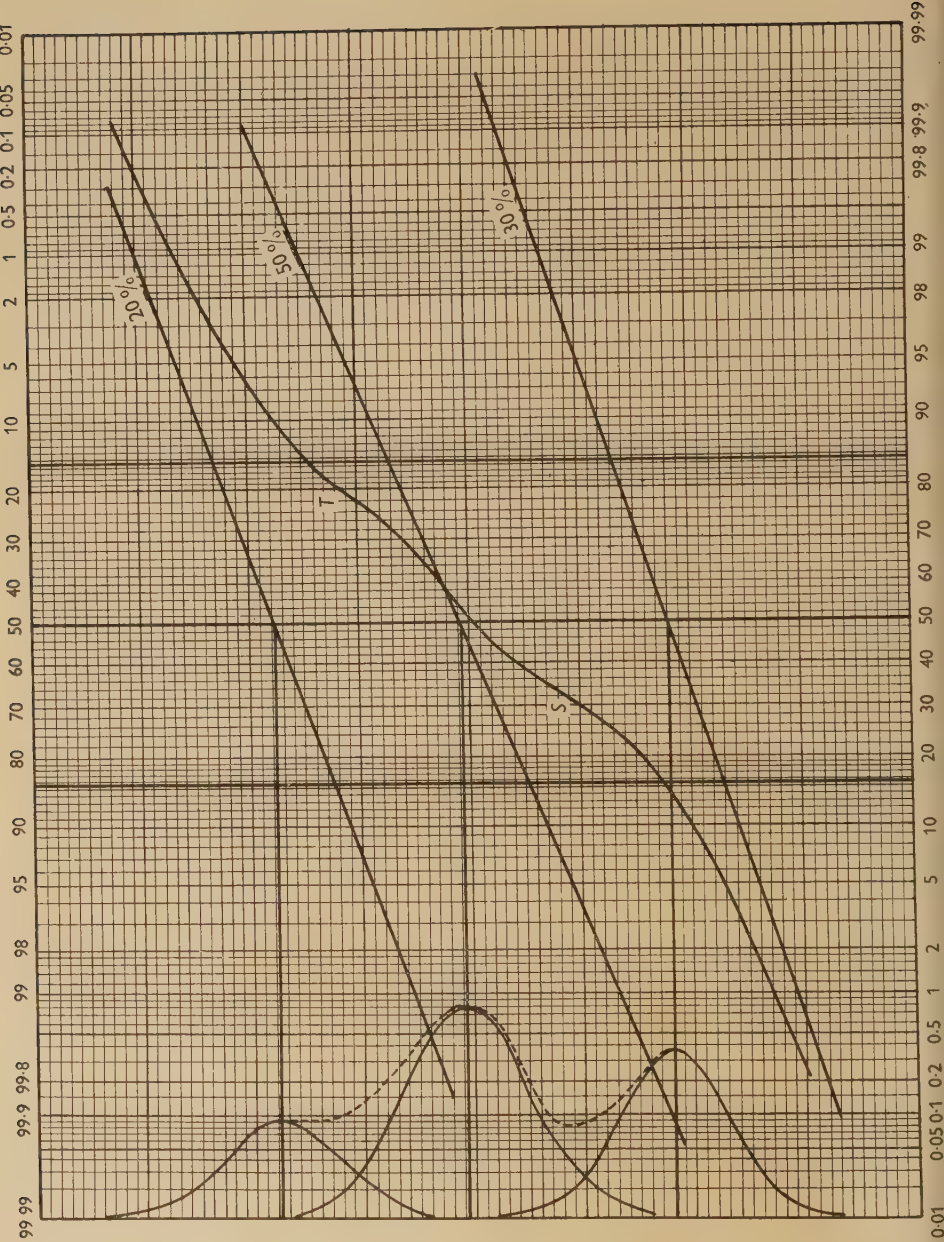
Fig. 3 gives the size distribution of 360 adult female copepods. The points when plotted on probability paper lie on an asymmetrically placed sigmoidal curve. There is a point of inflexion where the direction of curvature changes, on the 97 %:3 % vertical. This position for the point of inflexion suggests that there are two populations involved: a population of small individuals comprising 97 % of the sample, and mixed with them a small population of large individuals to make up the remaining 3 % of the sample. The lines *ST* and *QR* are accordingly drawn in to represent these two populations. The line *ST* is fitted by multiplying the percentages (read on the bottom scale) for the smallest individuals by 100/97 and the line *QR* by multiplying the percentages for the largest individuals (read on the top scale) by 100/3. The resultant of these two lines is the dotted line *UV*. The percentage at *Z* on this line, for example, is the sum of 3 % of the percentage at *X* and 97 % of the percentage at *Y*. In this example adjustment of the position of *QR* is unnecessary as the resultant fits the data well. The sample is analysed as representing two populations mixed in the proportions 97:3, with mean lengths of 1.223 and 1.477 mm. respectively, the standard deviations of both populations being about 50 μ .

Before leaving Fig. 3 I should like to draw attention to the abnormally

[illegible]

Fig. 3.

Polymodal curves are not difficult to analyse if the sample is large enough and the component populations do not overlap each other too much. Fig. 4 is drawn to show the effect of mixing three hypothetical populations in the



proportions 2:5:3. There are two points of inflexion at S and T , and these give the approximate proportions in which the populations are mixed, S occurring on the 30 % and T on the 80 % vertical, the difference between the two being 50 %. It is sometimes possible to analyse a polymodal curve even though there is considerable overlapping of the populations and there are no points of inflexion to guide one. Figs. 5 and 6 show two possible ways of analysing such a sample. The data analysed are the lengths of 1122 fish calculated by Ford (1928, p. 294), from the measurements of scales. Hodgson (Buchanan-Wollaston & Hodgson, 1929) considered that this population of fish 'certainly contains two modes at 12 cm. and about 15 cm.' He had reason to believe from experience with other samples that there was a third mode, he thought concealed between the two. We shall see that analysis by probability paper indicates a third, small population with a smaller mean length than either of the main populations. The sigmoidal shape of the distribution when plotted on probability paper is very similar in appearance to that of Fig. 1 and the data can be analysed as a symmetrical bimodal curve in the same way as Fig. 1 was. The resultant of the two lines shown fits the lengths of the fish above 13 cm. long very well and the fish below this length not quite so well. A better fit is shown in Fig. 6 where the upper tail of the distribution is fitted by a 20 % line. This leaves 30 % of the sample of fish to be fitted in between. By trial and error one finds that the only way of placing this line is at an angle to the other two as shown in Fig. 6. The resultant of these three lines is shown by the small x 's, while the circles are plotted from Ford's data. The agreement between the two is remarkable. The summation of the three distributions, shown as a dotted line superimposed on the histogram, also shows much better agreement with the sample than does the cruder analysis of Fig. 5. Table II gives the expected frequencies calculated from the results of Figs. 5 and 6 with the help of either Sheppard's tables or of tables of probits.

A χ^2 test for goodness of fit applied to these shows that the analysis of Fig. 5 is very unlikely to be true; but that the data are quite consistent with the analysis of Fig. 6, the probability of a χ^2 of 4.65 being about 0.2. In the calculations of χ^2 the classes for the 6.5 and 18.5 cm. have been bracketed together. A degree of freedom has to be subtracted for each mean, for each standard deviation, for all but one of the component populations and for the total. It is not claimed that the analysis of Fig. 5 gives the only possible, or even the best solution, indeed an attractive solution is the following:

- 50 % of the population with a mean 14.5 cm. and S.D. 1.3
- 40 % of the population with a mean 11.85 cm. and S.D. 1.1
- 10 % of the population with a mean 9.15 cm. and S.D. 0.9

The χ^2 summation for this solution is 7.95 which gives a value for $p = 0.048$. The goodness of fit is therefore not quite so good; but the ratio of the standard deviation to the mean for each population remains constant and this might be

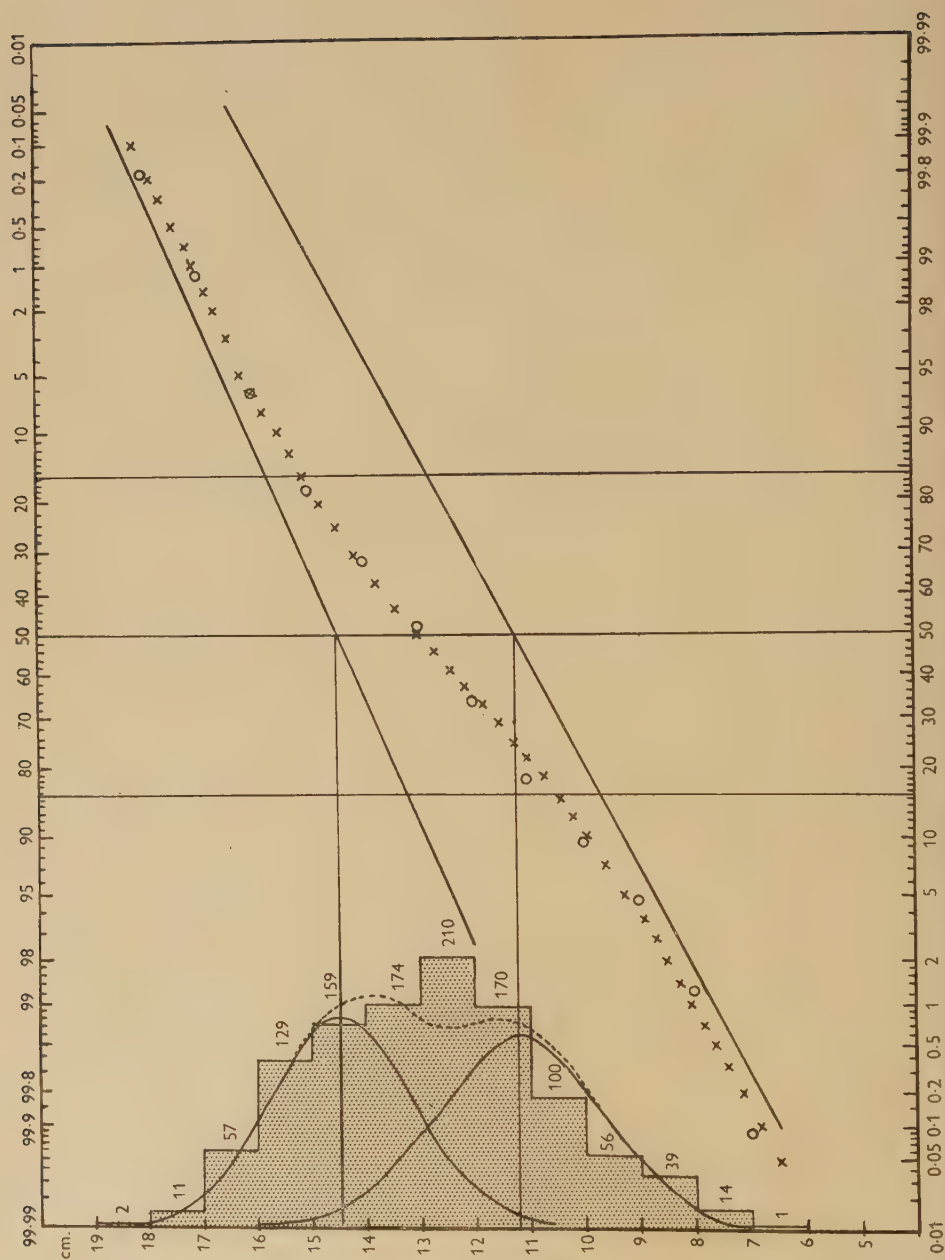


Fig. 5.

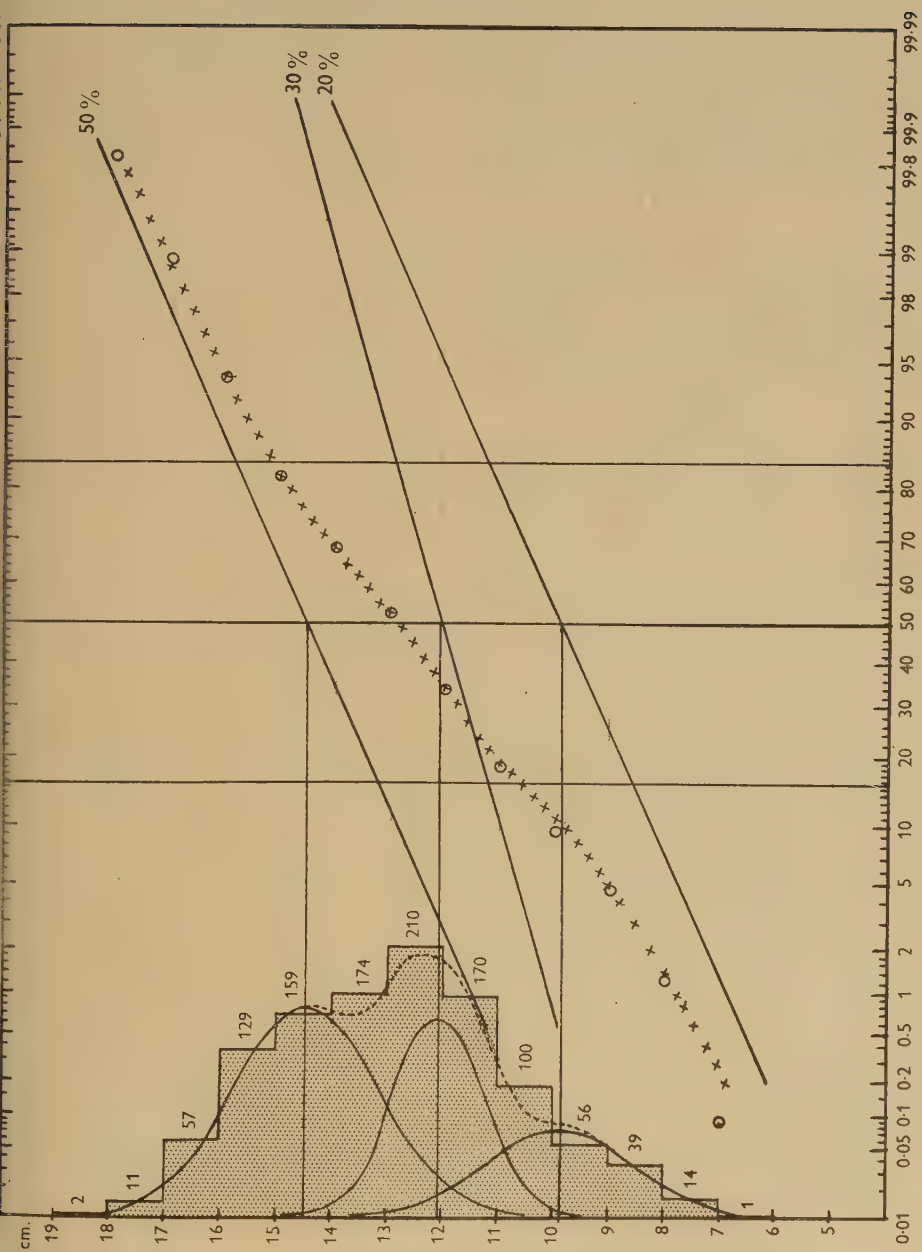


Fig. 6.

in its favour. I have chosen the solution of Fig. 5 for illustration because it is the more instructive in that given the other two lines the 30 % line has to be placed at an angle to them. In practice one would be guided by the biological nature of the material. If the three fish populations, for example, are three broods of the same year, there is no reason why one brood may not have hatched during a comparatively short season which might account for a small standard deviation for the size attained by winter.

TABLE II

Class (cm.)	Frequency obs.	Frequency calc. from Fig. 5			Frequency calc. from Fig. 6			
		50 %	50 %	Total	50 %	30 %	20 %	Total
		Mean ... 14.5	11.2		14.5	12.1	9.9	
		S.D. ... 1.3	1.505		1.3	0.8	1.3	
6.5	1	—	1	1	—	—	3	3
7.5	14	—	8	8	—	—	13	13
8.5	39	—	31	31	—	—	39	39
9.5	56	—	79	79	—	1	64	65
10.5	100	2	132	134	2	27	61	90
11.5	170	13	144	157	13	123	32	168
12.5	210	55	102	157	55	141	10	206
13.5	174	127	47	174	127	41	2	170
14.5	159	168	14	182	168	3	—	171
15.5	129	127	3	130	127	—	—	127
16.5	57	55	—	55	55	—	—	55
17.5	11	13	—	13	13	—	—	13
18.5	2	2	—	2	2	—	—	2
Total	1122	562	561	1123	562	336	224	1122

$$\chi^2 = 43.4, n = 6, p = < 0.001$$

$$\chi^2 = 4.65, n = 3, p = 0.2$$

When the component populations overlap as much as they do here one cannot expect a very precise analysis, but one is justified in saying that Ford's data show two main populations of fish with mean lengths of about 12 and 14.5 cm., and that there is in addition a small population whose mean length is between 9 and 10 cm. We may also estimate the standard deviations of the three fish groups to be of the order of 10 % of the respective mean lengths. An analysis which gives a satisfactory fit (Fig. 6) is only one of the simplest possible solutions, and is not necessarily the most complete picture of the facts, which may really conform to one of the many possible complex solutions. There may, for example, be many other small fish groups in the sample, and if both sexes are represented each of the three main groups are probably themselves bimodal in character. Neither the graphical method nor any other will give a complete and unequivocal solution; but fortunately the simplest solution is likely to be the most significant biologically, as well as statistically.

ACKNOWLEDGEMENTS

I am indebted to Dr G. A. Barnard, University of London, for bringing probability paper and its possibilities to my notice, and also to Mr W. F. Adams, Ministry of Transport, and Mr H. J. Joseph, Post Office Engineering Research Station, for their interest and help with the literature quoted.

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ON MANGANESE IN SEA AND FRESH WATERS

By H. W. Harvey, Sc.D., F.R.S.

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(Text-figs. 1-4)

Chemical and spectrographic analyses have shown that the sea contains a variable quantity of manganese, ranging between 1 and 10 mg./m.³ (Thompson & Wilson, 1935; Noddack & Noddack, 1940), while river waters contain some 500 to 1000 mg./m.³ (Twenhofel, 1938). These estimates include manganese in solution and that present as particulate or colloidal oxides soluble in concentrated hydrochloric acid.

In the deep waters of the oceans there is a continuous rain of manganese oxides falling on the ocean floor. Pettersson (1945) estimates that some 10 mg. of manganese may fall on each square metre annually.

In a previous communication it was shown that the sea off Plymouth contained, in 1946, insufficient manganese for the continued growth of several species of flagellates (Harvey, 1947). The experimental data, considered as a biological estimation of manganese in the water, indicated that the water contained only a fraction of 1 mg./m.³ in a form available to plant life.

These various observations indicate that the state of manganese in the sea—ionic, colloidal or particulate—and its distribution, are a pertinent subject for enquiry. Manganese is necessary for marine life. Sea waters obtained from different localities and depths are known to differ, the one from the other, in their capacity to support marine plant life irrespective of their content of available nitrogen, phosphorus and iron. It is not known what part, if any, varying concentrations of manganese *in an available form* may play in affecting the biological environment provided by the sea from place to place.

ESTIMATION OF MANGANESE SOLUBLE IN DILUTE ACIDS

The oxidation of tetramethyldiaminodiphenylmethane (*tetrabase*) in solutions containing periodate, to form a transient blue compound, is catalysed by traces of manganese. This reaction has been used by Nicholas (1946) to estimate this element in plant tissues. It was found possible to develop the method so that it could be used to estimate manganese in sea water to within a small fraction of a milligram per cubic metre of water.

The oxidation does not allow the estimation of manganese in solution in water at pH 8, since it can only be carried out in dilute acid, the *tetrabase* being insoluble in neutral solution. It is thought that the concentration of

manganese in the sea, present both in the ionic form and as colloidal or particulate oxides soluble at pH 4.7, should provide a fair index of the maximum concentration of manganese likely to be available to plants. Any colloidal micelles or particles which dissolve at a pH one or two units lower than that of natural sea water are likely to be available to plants, as is iron oxide (Harvey, 1937), the pH at the plant-water interface being lower than in the surrounding water (Danielli, 1944). On the other hand, particles which are insoluble in dilute acid are unlikely to be available, unless conditions at the plant-water interface are tantamount to a reducing medium, for which there is no evidence. (Particles of manganese oxides insoluble in dilute acid are readily soluble in an acidic reducing medium.)

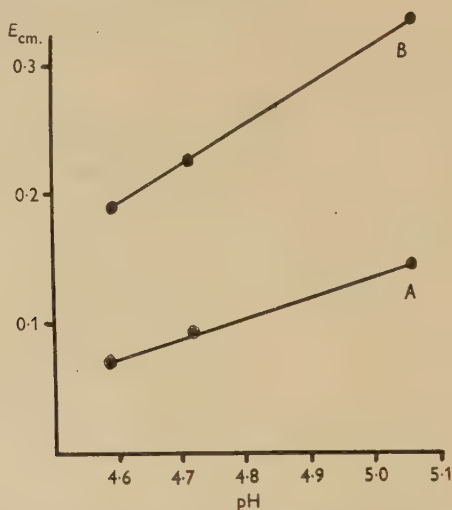


Fig. 1. Relation between pH and the extinction coefficient (E) in yellow light of the transient blue formed in sea water (A) and in the same sea water to which 3 mg. $Mn/m.^3$ had been added (B). Waters buffered with hydrochloric acid and ammonium acetate, and containing 50 mg. potassium periodate and 35 mg. tetrabase per litre.

When tetrabase is added to a solution containing periodate and manganese ions, oxidized to high valency by the periodate, a blue colour develops and quickly fades. In strongly acid solution the coloured oxidation product is unstable and is not formed. The intensity of blue colour formed depends upon the following factors:

- (i) *The concentration of tetrabase in solution.* This is very insoluble in neutral solution, its solubility increasing with increasing acidity.
- (ii) *The hydrogen-ion concentration.* With increasing acidity and the same concentration of tetrabase, less blue is formed (Fig. 1).
- (iii) *The concentration of periodate present.* It was also observed that less blue is formed when using a freshly made solution of periodate than with

a solution of the same concentration which has aged and started to smell of ozone. Ozone or ozonides play a part either in the oxidation of manganous-manganese or of the tetrabase.

Thus, of the reagents used, the periodate solution becomes more effective on aging, while the solution of tetrabase in acetone becomes less effective.

(iv) *The oxidation period*, or time during which the periodate has been mixed with the buffered sea water before mixing with tetrabase. Some evidence indicated that the oxidation of manganese ions to higher valency, having catalytic activity, is not quantitative but that an equilibrium mixture of polyvalent states is set up. This equilibrium mixture is unstable in buffered sea water, slowly reverting after an interval of time.

(v) *Salts in solution*. At the same pH and with the same concentration of periodate and tetrabase, the increase in blue developed due to unit addition of manganous salt was greater in water than in sea water, or in $3\frac{1}{2}\%$ sodium chloride solution.

(vi) *The nature and quantity of organic solvent in which the tetrabase has been dissolved*. The most satisfactory results have been obtained by adding the water and buffer and periodate to tetrabase dissolved in acetone, so that sufficient tetrabase is present to saturate fully the resulting mixture. If an excess of acetone is used, thereby increasing the solvency of the final mixture, no colour develops.

(vii) *Manganese present*. With solutions of a manganous salt in distilled water, containing up to 3 mg. Mn/m.³, and buffered with ammonium acetate and hydrochloric acid, a linear relation was found between the blue developed and the quantity of manganese present. An experiment such as is shown in Fig. 2 allows the 'reagent blank' to be calculated.

With lesser concentrations of tetrabase, the colour developed did not bear a linear relation to the quantity of manganese present, being proportionately less for greater than for smaller additions. From this observation it is concluded that there is a linear relation between the quantity of catalyst and the quantity of tetrabase transformed only when the concentration of the latter is at least 40,000 times that of the catalyst—about 10,000 times more molecules of tetrabase than of the catalytic manganese ions.

With sea water or sodium chloride, buffered at pH 4.6, to which manganese in quantity not exceeding 3 mg./m.³ had been added, the relation between blue formed and manganese present was not strictly linear with 130 mg./l. of tetrabase present (Fig. 3). This lack of linearity was found with 130 mg./l. of tetrabase at acidities varying between 4.5 and 5.0 pH and with a wide range of periodate concentrations.

This lack of linearity suggested that the salts in solution in the sea water affected the oxidation of the tetrabase by lowering its effective concentration relative to that of the active manganese. It was possible to increase the concentration of tetrabase to 200 mg./l. without causing turbidity by precipitation

in sea water, and probably to decrease the concentration of active manganese by adding less periodate.

Under these conditions the transient blue formed showed a linear relation to the quantity of added manganese salt (Fig. 4).

The procedure adopted in this experiment was as follows. There were added to 50 c.c. of sea water, from which most of the particulate matter had

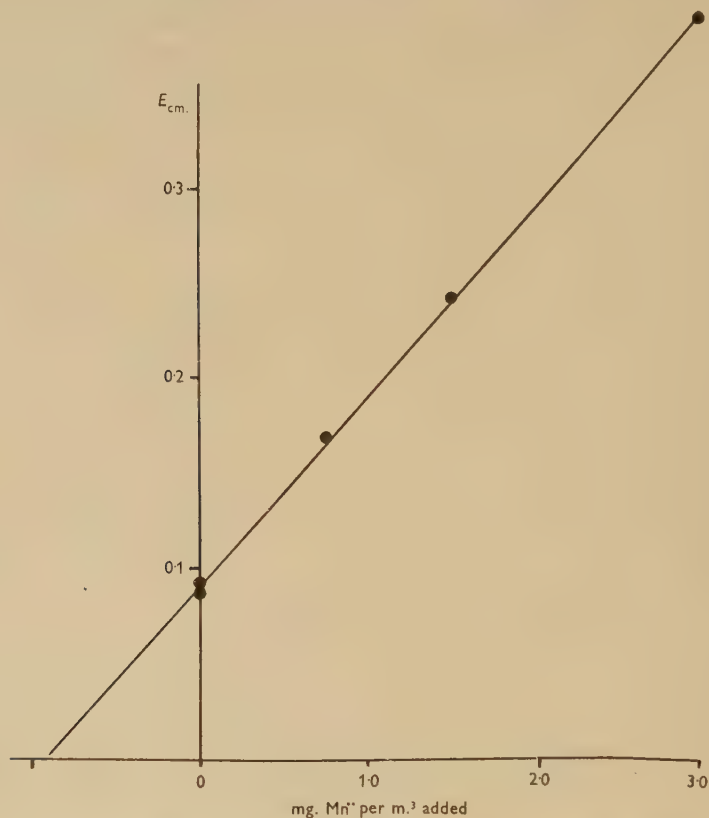


Fig. 2. The relation between the blue colour developed in distilled water, buffered at pH 4.8, and the quantity of manganese added. The extinction coefficients are of yellow light passing 'Ilford Spectrum 606' filters. Concentration of tetrabase, 130 mg./l.; of potassium periodate, 30 mg./l. Reagent blank deduced = 0.9 mg. Mn/m.³

settled during storage in a glass carboy, (i) 1.5 c.c. of hydrochloric acid *c.* 1.75 N, and 3 days later (ii) 1.5 c.c. of a solution of 100 g. ammonium acetate in 200 c.c. of water, and (iii) 3.7 c.c. of a solution containing 0.85 mg. potassium periodate (as found by titration in alkaline solution with sodium arsenite after adding potassium iodide). The oxidation of the manganous ions present was allowed to proceed for exactly 10 min. when the liquid was poured quickly into 4.5 c.c. of a 0.25% solution of tetrabase in acetone

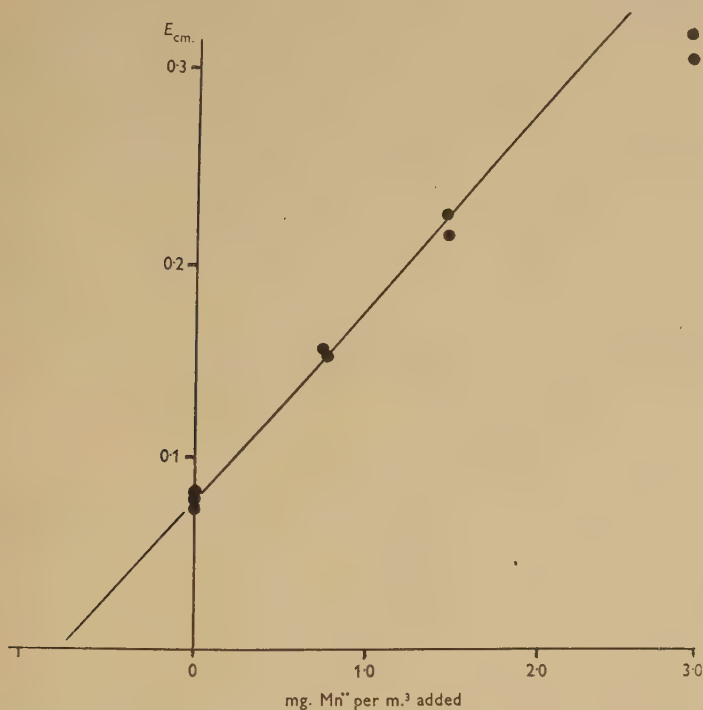


Fig. 3. Relation between colour formed and quantity of manganous salt added to sea water buffered at pH 4.6. Concentration of tetrabase, 130 mg./l.; of potassium periodate, 42 mg./l.

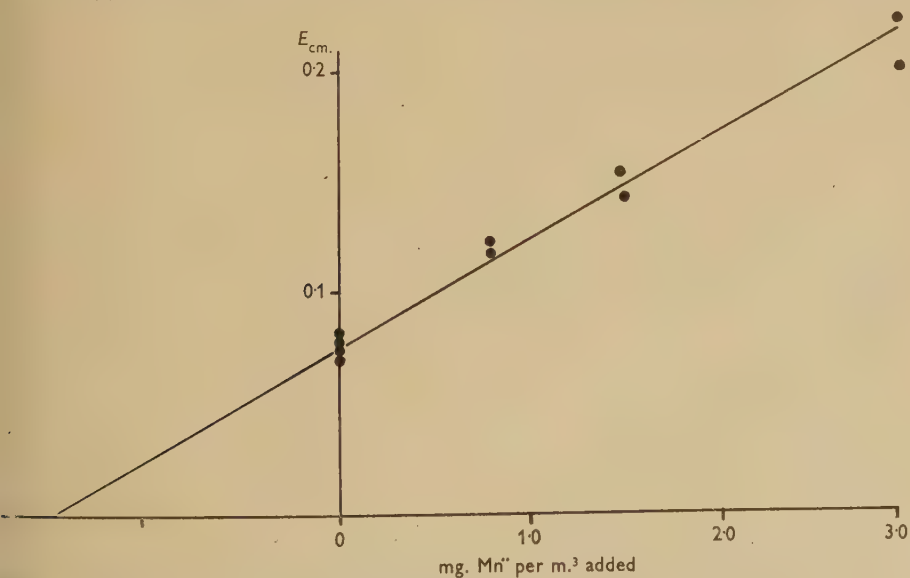


Fig. 4. Relation between colour formed and quantity of manganese salt added to stored sea water. Concentration of tetrabase, 200 mg./l.; of potassium periodate, 14 mg./l.

(freshly prepared). A glass cell was immediately filled and its optical density measured, as the blue colour attained its maximum some 40 sec. later at winter room temperature. Using a photoelectric absorption meter there was ample time to do this and follow the colour attaining its maximum, pausing and starting to fade.

The results of the experiment, as plotted in Fig. 4, indicate that the sea water and reagents contained 1.5 mg. Mn/m.³ Similar procedure with distilled water, using 3 c.c. of the tetrabase solution and the same buffers, provided a 'reagent blank' value of 1.25 mg. Mn/m.³. It is concluded from these estimations that the stored water contained 0.25 mg. Mn/m.³, originally present as manganese in true solution and as any colloidal or minute particles of hydrated oxides which dissolved during the 3 days at pH 1.3.

MANGANESE IN SEA WATER

A number of estimations of manganese in sea water collected off Plymouth have been made in the manner just described. The waters were either buffered and kept for a time to allow solution of manganese oxides at pH 4.6-4.75 or kept at pH 1.3 after adding the acid before adding the acetate.

It is seen from Table I that little more dissolves at pH 1.3 than at pH 4.6.

TABLE I

Time allowed for solution of manganese oxides before adding periodate	Estimated concentration of manganese in solution (mg. Mn/m. ³)
10 min. at pH 4.6	0.8
2 hr. at pH 4.6	0.9
24 hr. at pH 4.6	0.9
24 hr. at pH 1.3	1.0
Same water after storage for 14 days in a carboy	
4 days at pH 4.6	0.0
4 days at pH 1.3	0.2

It is notable that after storage in a carboy for 14 days the manganese, soluble in dilute acid, had decreased to a very low value. During this period, suspended plankton organisms and particles of organic detritus had sedimented and a growth of bacteria with some neritic diatoms had taken place, mostly on the glass surface. Thompson & Wilson's (1935) estimations of total manganese, which includes that soluble in hot concentrated acid, show that diatoms collect relatively large quantities of manganese. Adsorption of manganous ions or of colloidal micelles of hydrated oxides is indicated.

Experiment using the tetrabase method of estimation has shown adsorption of manganese ions from sea water enriched with a manganous salt on protein and even on filter-paper, but not on a clean glass surface.

The deposition of colloidal iron hydroxide on aquatic plants is a common phenomenon. Presumably colloidal and minute particles of oxide of manganese will tend to deposit on organisms in a similar manner.

The next series of estimations show a similar decrease in concentration of soluble manganese after 8 days' storage in a bottle, and further indicate that the adsorbed fraction is wholly eluted by acid at pH 1.3.

TABLE II. SEA WATER COLLECTED FROM A DEPTH OF 2 M. ABOUT 8 MILES OFF PLYMOUTH, 5 APRIL 1948

Time allowed for solution of manganese after adding acid at pH 1.3	Estimated mg. Mn/m. ³
20 hr.	0.85
8 days	0.8
Stored 8 days in bottle, then acid added to bottle	
3 hr.	0.9
Poured out of bottle after 8 days' storage before adding acid	
3 hr.	0.05, 0.7, 0.15

In subsequent estimations a buffer mixture was used, consisting of: 117 c.c. glacial acetic acid, 56 c.c. concentrated hydrochloric acid, 113 c.c. 0.880 ammonium hydroxide, 490 c.c. distilled water; and 3 c.c. were added to 50 c.c. of water.

This buffered sea water gave a lower 'reagent blank' value than the ammonium acetate mixture used previously.

In order to determine whether there was any marked difference in concentration of soluble manganese with depth of the water, the series of estimations shown in Table III was made.

TABLE III. WATER COLLECTED 20 MILES SEAWARD FROM PLYMOUTH ON 8 JUNE 1948, DEPTH 72 M.

Sample from (m.)	Time allowed for solution of manganese after adding buffer at pH 4.76	Estimated mg. Mn/m. ³
0.5	30 min.	1.1
5		0.9
25		1.0
50		1.1
70		1.1
Water collected from same position 30 June 1948		
5	20 hr.	0.75
50		0.3
Water collected 50° 00' N. 7° 10' W., 30 June 1948, depth 110 m.		
5	20 hr.	0.45
75		0.25, 0.3

The water occupying the area off Plymouth on 30 June contained less soluble manganese than samples collected earlier in the year. This water differed in other characteristics from that collected in the area during the previous and subsequent months, and in common with the water collected from 7° 10' W. it contained a considerably larger quantity of organic phosphorus.

I am indebted to Dr M. Parke for the information that the waters of Port Erin Bay, in the Isle of Man, usually contain a rich flora of flagellates during the summer months. In consequence, it was interesting to find whether these waters were richer in soluble manganese than those sampled in the mouth of the English Channel where the water contains fewer flagellates, since the growth of these plants is much affected by shortage of available manganese.

Mr J. R. Bruce kindly collected samples from the former locality, which on analysis gave the following estimates:

Collected from Port Erin Bay	mg. Mn/m. ³ after 24 hr. at pH 4.7
Sample <i>a</i>	2.2
Sample <i>b</i>	2.6
Sample <i>c</i>	2.0

In this usually flagellate-rich locality the water contained more than twice as much soluble manganese as the waters sampled in the English Channel.

MANGANESE IN FRESH WATERS

River waters are known to contain relatively large quantities of manganese. Twenhofel (1938) writes of 500–5000 mg./m.³ in streams, 'in which it is probable that the prevalent method of transportation of manganese is as oxide hydrosols stabilized by organic colloids'.

It was of interest to find how much of this total was in the form of manganese soluble in dilute acid, and how this varied with the nature of the stream.

Samples of natural waters were collected in June 1948, those from the Lake District by Mr F. J. Mackereth who also kindly supplied the appended particulars relating to the usual planktonic life in the six waters. The results of examining these samples are given in Table IV.

It is noteworthy that the readily acid-soluble manganese varies in the waters from the Lake District in roughly the same order as their productivity. It seems improbable that the manganese content in any way controls the productivity, but more likely that it is affected by those factors which themselves control plant and animal growth. Heintze & Mann (1946) find that more manganese can be washed out from agricultural soils containing greater quantities of organic matter than from soils containing less organic matter. Moreover, addition of organic compounds to the water increased the manganese in the leachate.

TABLE IV. MANGANESE IN SAMPLES OF RIVER AND LAKE WATER

Locality	mg. Mn/m. ³ soluble after 24 hr. at pH 4.7
Devonshire:	
River Yealm at Wisdome on leaving moorland	1.15
River Yealm at Yealm Bridge after passing through some 7 miles of agricultural country	10
Plymouth tap water (moorland reservoir)	1.8
Lake District:	
Esthwaite. 'A very productive lake' surrounded by agricultural land	> 40
Bellham Tarn. 'A small lake containing a good supply of nutrients but not so productive as Esthwaite'	20
Black Beck. Stream feeding Esthwaite and bringing in most of the nutrients	12
Windermere (North Basin). Of fairly high productivity for diatoms, but few blue-green algae	10
Loweswater. A lowland lake lying in agricultural land and usually fairly productive	11 (after 44 hr. 11, 7.5)
Ennerdale. Usually very poor in planktonic organisms and has low concentrations of nutrients	6.5, 8 (after 44 hr. 8, 8.5)

SUMMARY

A method of estimating the maximum quantity of manganese available to plants in sea and fresh waters is described.

Samples of sea water collected off Plymouth in 1948 contained 0.7–1.0 mg. Mn/m.³ in solution plus any particles soluble at pH 4.6. After storage and sedimentation of particulate matter, the quantity decreased to 0.0–0.25 mg./m.³

Samples collected off the Isle of Man, an area with a rich summer population of flagellates, contained 2.0–2.6 mg./m.³

The river Yealm, south Devon, on leaving Dartmoor contained 1 mg., and after passing through agricultural land 10 mg./m.³

Lakes and streams in the English Lake District contained 6–40 mg./m.³. The least fertile waters contained the least soluble manganese.

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THE BIOLOGY OF *ASTERIAS RUBENS* L.: GROWTH AND REPRODUCTION

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(Text-figs. 1-5)

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INTRODUCTION

The morphology and embryology of the common starfish, *Asterias rubens* L., have been extensively studied, but its general biology and, in particular, the details of its sexual maturity and spawning, have hitherto been largely neglected. This is the more surprising since the species is one of considerable negative economic importance, being a voracious consumer of marketable lamellibranchs and a competitor for food with many bottom-feeding fishes.

In the present work an attempt has been made to follow the cycle of gonad changes which occur throughout the year in populations of *A. rubens* occurring in the English Channel off Plymouth, and also to obtain data on its rate of growth, the relation between size and maturity and the factors influencing the onset of sexual maturity.

DISTRIBUTION, HABITAT AND FOOD

A. rubens is distributed throughout the north-east Atlantic from high water to a depth of 400 m., sometimes to 650 m. The geographical limits of its distribution are to the north, the White Sea and Iceland; to the east, the Baltic; and to the south, the coast of Senegal. It is not found off Greenland and only accidentally in the Mediterranean (Mortensen, 1927).

In his survey of the bottom fauna near the 30-fathom line from Eddystone and Start Point in south Devon, Allen (1899) found that it occurred on nearly all the grounds, varying from mud to coarse and shelly gravel and rock,

although there were considerable differences in its abundance on the various substrata. He also observed that in this area its distribution was closely correlated with that of *Chlamys opercularis* (L.) which provides a large part of its food.

While still in a young stage it eats barnacles and small lamellibranchs. As an adult it feeds chiefly on worms, crustaceans, other echinoderms and many lamellibranchs, in particular *C. opercularis* and *Mytilus edulis*. In fact, it would appear to be omnivorous, eating any living or dead animal material on which it can get a firm hold.

POPULATIONS OF *ASTERIAS RUBENS* OFF PLYMOUTH

As is usual with asteroids, size is expressed in the following study in terms of radius length, measured from the anus to the tip of the longest arm. The starfishes were all measured living, out of water, on a flat bench, so that each arm could be flattened out and straightened before measurement. Arm measurements (denoted as R =radius length) were taken to the nearest millimetre, except those of starfishes with R greater than 20 cm., where arm contraction and expansion made the readings only accurate to the nearest 0.5 cm.

Records were also kept of the length of the gonad in each measured arm. These measurements were taken from the central point of the blunt proximal end of the gonad to the tip of the most distal tubule. At the same time smears of each gonad measured were examined microscopically, and sections were cut of a number of gonads in each sample.

The difference in size composition of populations living under different conditions is clearly brought out by a comparison of the two main populations of *A. rubens* studied. The first population occurs on the Rame-Eddystone Grounds on a mixed substratum of sand and rough ground at a depth of 25-30 fathoms. The second population, which will be termed the Outer Grounds population, occurs some miles away to the south and south-west of Eddystone. The sea bottom in this area is largely composed of sand with patches of gravel, and it shelves gradually from a depth of 64 m. 3 miles south of Eddystone to 70 m. at 6 miles south. The routine hauls for starfishes were all taken with an otter trawl.

The Rame-Eddystone Grounds Population

The means and ranges of the starfish samples taken in this area are shown in Table I. It will be seen that there are certain differences between one catch and another not always consistent with the period at which they were taken; for instance, the catch for 24 June 1947 has a lower size range and mean than that for 13 June 1947. This is to be expected in a species where growth is so directly dependent upon available food, and where it may cease altogether in places where the food supply is poor. It would not be possible with present

bottom-sampling techniques to obtain periodic representative samples from any one small section of the main area, nor was such attempted.

TABLE I. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* ON RAME-EDDYSTONE GROUNDS

Date	Total in catch	Males				Females				Sex not known
		No.	Range	Mean	σ_M	No.	Range	Mean	σ_M	
1. i. 47	58	27	4.0-15.9	9.24 ± 0.56		28	4.0-13.9	9.43 ± 0.48		3
4. ii. 47	30	15	4.0-12.9	8.70 ± 0.67		12	4.0-14.9	9.75 ± 1.06		3
27. iii. 47	44	16	3.0-13.9	8.50 ± 0.74		19	3.0-14.9	8.66 ± 0.63		9
16. iv. 47	41	10	5.0-15.9	8.30 ± 1.11		18	5.0-14.9	9.33 ± 0.61		13
23. iv. 47	87	34	3.0-14.9	8.79 ± 0.38		42	5.0-13.9	9.45 ± 0.33		11
13. vi. 47	33	14	8.0-13.9	11.15 ± 0.32		16	6.0-15.9	11.13 ± 0.68		3
24. vi. 47	35	11	5.0-14.9	9.60 ± 0.91		23	7.0-16.9	11.02 ± 0.52		1
2. vii. 47	78	33	5.0-22.0	13.40 ± 0.57		38	7.0-17.9	12.66 ± 0.22		7
3. vii. 47	50	18	6.0-21.0	11.00 ± 0.77		22	7.0-15.9	11.77 ± 0.45		10
24. vii. 47	42	15	3.0-16.9	9.70 ± 0.82		19	5.0-15.9	10.13 ± 0.69		8
25. vii. 47	40	19	3.0-16.9	9.66 ± 0.84		12	5.0-17.9	9.83 ± 0.96		9
7. viii. 47	68	30	7.0-16.9	11.27 ± 0.39		35	5.0-15.9	11.30 ± 0.47		3
19. viii. 47	78	27	3.0-16.9	10.98 ± 0.59		44	6.0-24.0	12.05 ± 0.51		7
11. ix. 47	77	28	3.0-17.9	10.43 ± 0.64		45	3.0-14.9	9.66 ± 0.42		4
28. x. 47	38	12	6.0-15.9	11.32 ± 0.82		18	8.0-15.9	11.28 ± 0.45		8
17. xi. 47	38	19	5.0-18.9	11.08 ± 0.81		18	5.0-16.9	10.56 ± 0.79		1
16. i. 48	49	23	4.0-14.9	9.98 ± 0.61		26	4.0-15.9	10.35 ± 0.61		0
10. ii. 48	41	21	4.0-15.9	9.74 ± 0.64		13	4.0-13.9	8.35 ± 0.79		7
23/24. iii. 48	61	23	4.0-15.9	10.14 ± 0.70		32	4.0-18.9	10.47 ± 0.54		6
11. v. 48	68	28	4.0-18.9	11.46 ± 0.57		38	5.0-17.9	10.50 ± 0.50		2
7. vi. 48	50	25	6.0-17.9	10.78 ± 0.53		25	6.0-17.9	11.30 ± 0.55		0
21. vi. 48	110	58	5.0-16.9	11.57 ± 0.36		52	5.0-19.9	11.13 ± 0.40		0
	1216	506				595				115

TABLE II. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* ON OUTER GROUNDS

Date	Total in catch	Males				Females				Sex not known
		No.	Range	Mean	σ_M	No.	Range	Mean	σ_M	
20. iii. 47	33	12	6.0-16.9	12.50 ± 0.90		21	9.0-21.9	14.60 ± 0.61		0
9. iv. 47	29	11	8.0-18.9	12.68 ± 1.02		13	7.0-19.9	13.27 ± 0.85		5
18. iv. 47	50	25	11.0-19.9	14.86 ± 0.43		25	9.0-21.9	15.66 ± 0.52		0
25. iv. 47	175	66	5.0-18.9	14.21 ± 0.32		105	6.0-18.9	15.05 ± 0.21		4
23. v. 47	57	17	9.0-15.9	12.26 ± 0.47		39	8.0-16.9	12.35 ± 0.33		1
16. vi. 47	101	44	10.0-22.9	15.84 ± 0.43		57	11.0-23.9	16.45 ± 0.33		0
4. vii. 47	213	83	8.0-19.9	14.79 ± 0.27		127	8.0-21.9	15.49 ± 0.25		3
16. vii. 47	172	89	7.0-21.9	16.56 ± 0.28		79	8.0-22.9	16.92 ± 0.36		4
27. viii. 47	151	63	9.0-19.9	14.29 ± 0.30		85	8.0-22.9	14.88 ± 0.28		3
21. x. 47	71	36	6.0-22.9	14.72 ± 0.51		34	10.0-21.9	15.88 ± 0.48		1
13. xi. 47	39	19	13.0-26.9	18.55 ± 0.93		20	12.0-33.9	17.95 ± 1.02		0
15. i. 48	29	15	5.0-22.0	14.03 ± 1.19		14	10.0-21.8	15.36 ± 0.95		0
4. ii. 48	15	7	9.0-21.5	13.64 ± 1.53		8	7.1-16.1	12.0 ± 1.03		0
12. iii. 48	38	15	5.9-16.6	12.23 ± 0.76		20	8.9-18.8	14.35 ± 0.61		3
14. iv. 48	103	50	8.0-20.0	14.34 ± 0.38		53	7.6-20.5	15.88 ± 0.43		0
13. v. 48	231	87	10.5-23.8	16.89 ± 0.32		144	8.8-25.5	18.51 ± 0.25		0
11. vi. 48	148	64	7.5-17.8	13.48 ± 0.32		84	6.2-23.5	13.44 ± 0.32		0
6. vii. 48	90	38	8.4-21.5	14.24 ± 0.52		52	7.6-21.5	14.98 ± 0.42		0
11. viii. 48	50	20	11.1-22.2	15.00 ± 0.66		30	9.6-27.5	15.6 ± 0.73		0
	1795	761				1010				24

The Outer Grounds Population

The means and ranges of the starfish samples taken in this area are shown in Table II. This shows clearly the overall larger sizes of the starfishes in this area, compared with those in the Rame-Eddystone Grounds.

The Population near E 1

A smaller number of samples was taken by trawling in the grounds near International Station E 1 (10 miles S.W. of Eddystone). The means and sizes of these samples are shown in Table III. The starfishes taken in this area are still larger than those on the Outer Grounds.

TABLE III. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* NEAR E 1

Date	Total in catch	Males				Females			
		No.	Range	Mean	σ_M	No.	Range	Mean	σ_M
3. vi. 47	168	44	11.0-23.9	17.98 $\pm$ 0.42		124	11.0-30.9	20.36 $\pm$ 0.31	
10. vi. 47	19	7	16.0-20.9	18.64 $\pm$ 0.49		12	18.0-23.9	20.75 $\pm$ 0.40	
17. vi. 47	39	9	14.0-21.9	19.38 $\pm$ 0.77		30	15.0-27.9	21.37 $\pm$ 0.57	
15. ix. 47	50	21	14.0-27.9	20.16 $\pm$ 0.72		29	15.0-28.9	21.43 $\pm$ 0.69	
	276	81				195			

The Cawsand Bay Population

A single haul was obtained from this area on 23 May 1947, and it consisted of 18 small starfishes. The means and range of the starfishes in this haul were:

	No.	Range	Mean (cm.)
Males	8	3.0-4.0	3.7
Females	10	3.0-8.4	4.3

The Plymouth Sound Population

In spring 1948 a new and very large population of *A. rubens* was found on Asia Grounds in Plymouth Sound, 800 m. W.S.W. of the Plymouth Laboratory. A small sample was obtained on 10 February 1948 and a larger one on 16 April 1948, both of which were examined for size and gonad maturity. The means and size ranges of these samples are shown in Table IV.

TABLE IV. ANALYSIS OF HAULS OF *ASTERIAS RUBENS* ON ASIA GROUNDS IN PLYMOUTH SOUND

Date	Total in catch	Males				Females			
		No.	Range	Mean	σ_M	No.	Range	Mean	σ_M
10. ii. 48	25	11	8.3-11.0	9.50 $\pm$ 0.08		14	6.6-10.1	8.79 $\pm$ 0.28	
16. iv. 48	100	52	5.9-18.4	9.30 $\pm$ 0.28		48	6.0-11.8	9.54 $\pm$ 0.21	
	125	63				62			

In addition to these samples, hauls were also made on 3 and 4 March 1948. On 3 March three 40-min. trawl hauls were made and the total catch was

95 *A. rubens*. On 4 March four 40-min. trawl hauls yielded a total catch of 1259 *A. rubens*.

This population was undoubtedly the most homogeneous of those examined, and it was found to be feeding entirely on very rich beds of mussels (*Mytilus edulis*). In contrast with the starfishes caught outside Plymouth Sound, which were red-brown or more rarely pale yellowish brown in colour, the starfishes from Asia Grounds were, without exception, a bright red colour. In addition, there was a marked difference in body shape. Starfishes from the Rame-Eddystone and Outer Grounds had thin, gradually tapering arms, whereas the Asia Grounds population had thick robust arms which tapered only in the distal part. These very distinct differences may be correlated with the differences in food supply of the starfishes from the two areas.

The Rame Mud Population

A single haul was taken with an Agassiz trawl on the Rame mud, 2 miles W.S.W. of Rame Head in 26 fathoms. Although the catch with this trawl is not strictly comparable with those taken with the otter trawl, it is interesting to note that no medium or large starfishes were taken, although these sizes have often been taken with an Agassiz trawl working on the Outer Grounds. The starfishes taken on the mud were all small or very small, with thin arms, coloured dark red-brown. The mean and range for the starfishes in this haul were:

Date	Total in catch	Range (cm.)	Mean (cm.)
7. iv. 48	95	1.0-6.4	2.52

The above data are for both sexes, as the specimens in this catch were mostly so small and underdeveloped to allow the sex to be determined accurately.

Comparison of the Size Compositions of the Populations

The means and ranges have been used only to characterize the starfish populations of the different grounds, and it will be seen from Fig. 1 that the differences are marked. This graphical representation of the samples shows that, apart from the marked difference between the means, there was in the Outer Grounds a complete lack of the size classes *R* 3-5 cm. and a scarcity of the size classes 7-10 cm.; and this in spite of the large number of individuals taken in many of the Outer Grounds hauls. These size classes are all present in reasonable numbers in the Rame-Eddystone samples. This difference between the two sets of samples cannot be due to selective fishing by the trawl. It is unlikely that the same fishing gear used over similar substrata would select large and medium starfishes in the Outer Grounds and small and medium sizes on the Rame-Eddystone Grounds if all three size groups were present in each area. It is considered that the trawl brings up from each ground a random sample of all those sizes which are present, with the exception of the smallest sizes (*R* under 3 cm.). These smaller sizes were, in fact, present on

the Rame-Eddystone Grounds in the spring and summer of the year, when they were caught in a few dredge hauls. They were not found on the Outer Grounds until about October, when a few small (R ca. 3–6 cm.) starfishes were taken.

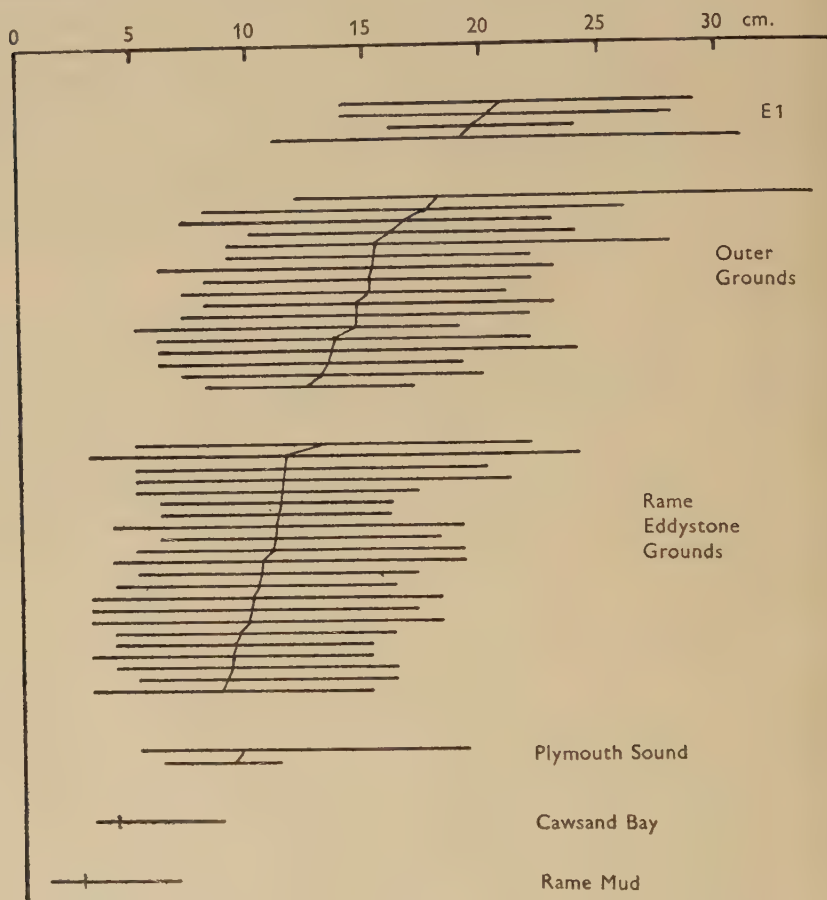


Fig. 1. Size ranges and means (in cm.) of six starfish populations off Plymouth.
(Means joined by vertical lines.)

There are two possible explanations for the absence from the Outer Grounds of the small (R 3–6 cm.) sizes. First, the 1946 starfish spat might have failed to settle in the Outer Grounds. This is very unlikely in view of the large breeding population on these grounds. But secondly, a proportion of the 1946 brood may have settled successfully in the Outer Grounds and prospered so well on the rich food there that by March–April 1947 they had already reached and passed the 6 cm. size class. This would mean that by April 1947 there would be few, if any, starfishes with a radius length of less than 6 cm.

remaining on the Outer Grounds, and the chances of catching them in trawl or dredge would be slight. On this view it would be necessary to postulate radial growth of a least 6 cm. (and probably more) in the 9 months between metamorphosis in July 1946 and April 1947; that is, an average monthly increment of rather less than one centimetre. That this is quite possible is shown by the laboratory observations on rate of growth in *Asterias rubens* recorded below.

The Plymouth Sound starfishes caught in 1948 could not have been younger than the 1947 brood, and they show means of $R=9.4$ cm. for the males and $R=9.2$ cm. for the females. This very homogeneous population was almost certainly made up of one year-group only, and, again on the basis of laboratory observations, it is considered that they did, in fact, belong to the 1947 brood. A large concentrated starfish population such as this, feeding on an abundant fixed food supply, will tend to remain localized in space and its individuals will be likely to grow at approximately similar growth rates so long as the food lasts. When the food is depleted the population will disperse and the growth rate of the individual starfishes will then become variable, leading to a population which is heterogeneous in size composition.

In contrast, the Rame Mud population with a mean $R=2.5$ must also have been at least 10 or 11 months old, and probably represented the remains of one or more spatfalls which had fallen on a bottom poor in available starfish food.

GROWTH RATE

During 1947 a number of starfishes taken on the Rame-Eddystone Grounds or from weed collected in Plymouth Sound were kept in laboratory tanks with an excess supply of graded sizes of *Mytilus edulis*, *Tellina crassa* and *Chlamys perpectus*. After about a week the starfishes became acclimatized to aquarium conditions and started feeding voraciously. Measurements of radius length were taken at intervals, and results are shown in Table V. (No attempt was made in these preliminary experiments to record the quantity of food consumed by each individual starfish, although further work on this subject is now in progress.) The data in Table V are shown graphically in the form of growth curves in Fig. 2. Growth is fastest during the summer, when the monthly increment may exceed 1 cm. Even during the winter growth continues, although at a reduced rate, and a further increase in rate occurs in spring.

Most of these observations were made on starfishes which were caught onshore in summer 1947 at sizes between 4 and 8 cm. radius. Assuming that these belonged to the 1946 brood, they must have been growing at an average rate of 0.5 cm. per month since metamorphosis 11 or 12 months before. When fed with unrestricted supplies they grew at a somewhat faster rate. Thus starfish B 11, caught and measured as 4.4 cm. R on 10 August, had reached 7.2 cm. R by 30 November. This is an increment of 4.8 cm. in $3\frac{3}{4}$ months, or

an average of 1.2 cm. per month. This was a fast summer rate and growth decreased from November onwards. The curves show that growth in this starfish and in other similar ones was not steady, but that it appears to have proceeded in a number of steps. This may, of course, have been due to slight errors in measurement.

TABLE V. GROWTH MEASUREMENTS FOR WELL-FED INDIVIDUALS OF *ASTERIAS RUBENS* IN CM.

	B 1	B 2	B 3	B 4	B 5	B 6	B 7	B 8	B 9	B 10	B 11	B 12	B 13	B 14	B 15	BB 9
26. i. 47	5.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2. ii. 47	6.0	3.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16. ii. 47	6.2	3.6	4.4	—	—	—	—	—	—	—	—	—	—	—	—	—
2. iii. 47	6.4	3.7	4.7	3.0	—	—	—	—	—	—	—	—	—	—	—	—
6. iv. 47	7.2	4.3	5.5	4.1	—	—	—	—	—	—	—	—	—	—	—	—
13. iv. 47	7.6	4.3	5.5	—	—	—	—	—	—	—	—	—	—	—	—	—
27. iv. 47	—	4.5	5.9	—	7.2	—	—	—	—	—	—	—	—	—	—	—
4. v. 47	—	4.8	6.1	—	7.4	—	—	—	—	—	—	—	—	—	—	—
25. v. 47	—	5.4	7.1	—	8.0	6.0	—	—	—	—	—	—	—	—	—	—
1. vi. 47	—	—	7.4	—	8.0	6.4	4.8	—	—	—	—	—	—	—	—	—
29. vi. 47	—	—	8.3	—	9.4	7.3	5.7	—	—	—	—	—	—	—	—	—
6. vii. 47	—	—	8.6	—	—	7.7	6.1	1.3	—	—	—	—	—	—	—	—
20. vii. 47	—	—	8.8	—	—	8.3	6.7	1.8	1.0	—	—	—	—	—	—	—
10. viii. 47	—	—	9.7	—	—	9.0	7.6	2.3	1.4	8.6	4.4	4.2	—	—	—	—
17. viii. 47	—	—	9.8	—	—	9.6	8.3	2.8	1.6	8.7	4.5	4.2	7.8	5.8	—	—
24. viii. 47	—	—	9.8	—	—	10.1	—	3.0	2.0	8.9	4.9	4.6	8.0	6.1	—	—
7. ix. 47	—	—	—	—	—	10.5	—	3.1	2.2	10.2	5.6	5.1	8.6	7.0	—	—
21. ix. 47	—	—	—	—	—	11.2	—	3.9	2.7	11.0	6.6	5.3	9.2	8.1	—	—
28. ix. 47	—	—	—	—	—	11.3	—	—	2.8	11.7	7.3	—	9.4	8.8	—	—
26. x. 47	—	—	—	—	—	11.9	—	—	3.2	12.4	8.7	—	—	10.3	6.3	—
2. xi. 47	—	—	—	—	—	11.9	—	—	3.4	—	8.8	—	—	10.4	6.3	—
30. xi. 47	—	—	—	—	—	—	—	—	4.5	—	9.2	—	—	10.7	6.9	—
7. xii. 47	—	—	—	—	—	—	—	—	4.8	—	9.3	—	—	—	7.0	—
14. xii. 47	—	—	—	—	—	—	—	—	5.0	—	9.3	—	—	—	7.0	—
4. i. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.8
1. ii. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10.7
7. iii. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11.3
14. iii. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11.3

A few growth curves were obtained for starfishes almost certainly belonging to the 1947 brood. Starfish B 9 was caught on 20 July 1947 on a clump of *Mytilus edulis* and it then measured 1 cm. *R*. By 7 December 1947 it measured 4.8 cm., an increment of 3.8 cm. in $3\frac{2}{3}$ months, or about 1 cm. (average) per month. Some idea of the size likely to have been reached by starfish B 9 by April 1948 may be obtained by referring to the growth curve of another well-fed starfish B 1 which measured 5.9 cm. *R* on 26 January 1947. By 13 April 1947 this starfish had grown to 7.6 cm. *R*, an increment of 1.7 cm. in $2\frac{1}{2}$ months, or an average (winter) monthly increment of 0.7 cm.

From the present observations on growth rate it is clear that small and very small starfishes (up to at least 6 cm. *R*) can grow at a monthly rate of rather more than 1 cm. in summer and autumn and of rather less than 0.5 cm. in winter. These rates are only attained when the food supply is abundant.

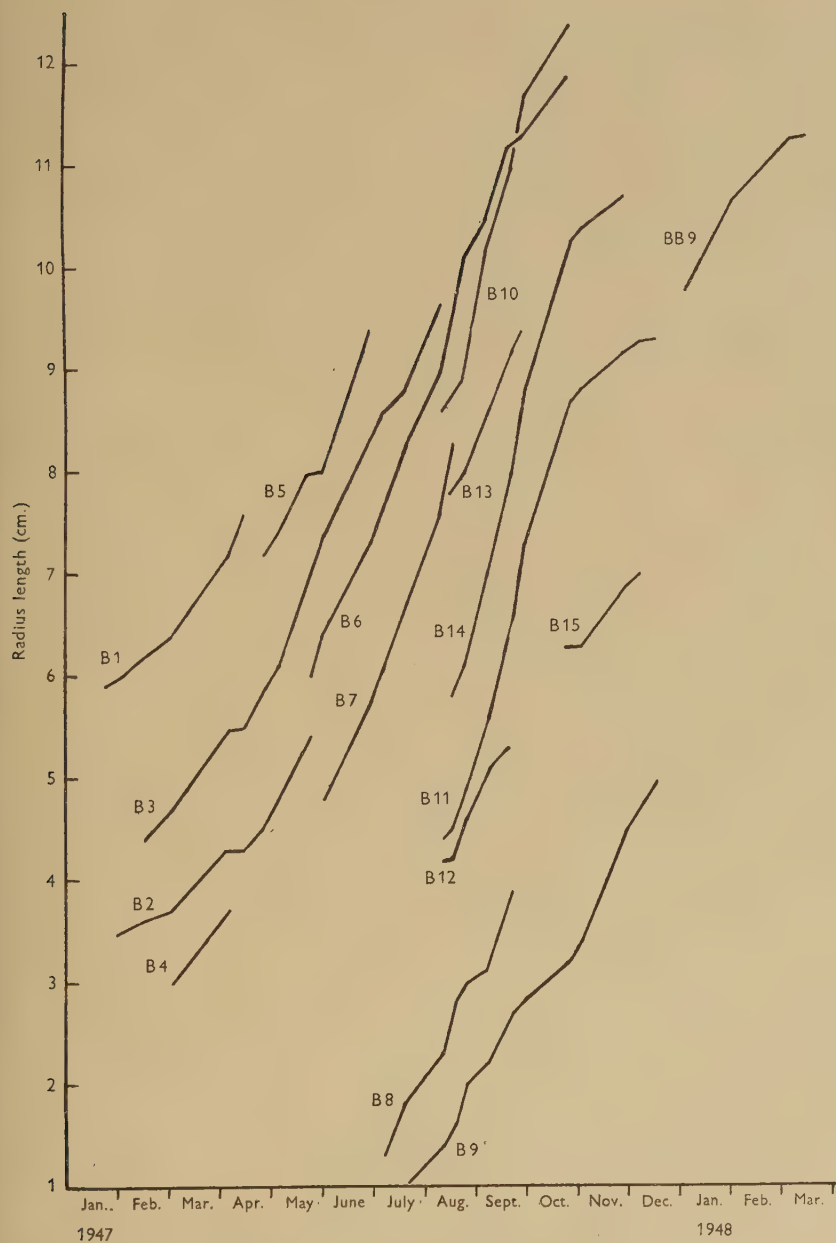


Fig. 2. Growth curves of well-fed *A. rubens* plotted from Table V.

These results may be compared with the observations of Orton & Fraser (1930), who examined a sample of 1800 young *Asterias rubens* taken from a buoy near Liverpool on 30 May 1930. Their method of measurement differed from that used in the present work; they expressed size in terms of the length of a straight line joining the tips of alternate arms. Their values for size have been converted to conform with those used in this study. In addition, their measurements were taken on preserved specimens, and they suggested that in life their values would have been on an average 5 mm. larger; allowance has also been made for this factor. They found that the modal value of their sample was 2.2 cm. *R* with a range from 0.6 to 5.2 cm., and, knowing the date on which the buoy had been placed in position, they reckoned that this amount of growth had taken place in rather less than a year. On this information, therefore, the monthly increment of the starfishes round the mode was about 0.25 cm., and the maximum monthly increment a little more than 0.5 cm. Their population appears, therefore, to have been growing considerably slower than those observed in the laboratory experiments. However, the total sum of conditions in the two sets of starfishes is not strictly comparable. The population of Orton & Fraser, although surrounded by a plentiful supply of young growing mussels, would have been subject to the action of waves and wind, and there may have been competition for suitably sized food as the population grew. In the laboratory experiments, on the other hand, there were no severe external physical factors except the seasonal decrease in temperature in winter, and also probably no food competition. Furthermore, in the buoy population, although the very small sizes would have no difficulty in hiding away among the mussels in rough weather, the larger starfishes will have presented a greater surface area to the action of the waves. Some of them may therefore have been washed off the buoy, thus reducing the modal value and upper range limit of the population sample. It is considered that the conditions obtaining in the laboratory experiments more closely resembled those on a sea bottom area rich in food than did those in the population on the floating buoy.

Mead (1899), working on the closely related species *A. forbesi* Desor, also found that the rate of growth in young specimens fed on plentiful supplies of lamellibranchs was fast and strictly comparable with the present observations. One of his starfishes, which measured about 1.8 cm. on 18 August, was fed on abundant food and had reached a size of 3.5 cm. *R* by 26 September, a rate similar to that shown by starfish B 9 of the present observations. Further observations on growth in *A. forbesi* are given by Galtsoff & Loosanoff (1939).

Growth Rate in Poorly-fed Starfishes

As control to these experiments a number of starfishes were kept in a separate tank with a minimum of food (a few small barnacles only). They were measured periodically and it was found that no measurable growth occurred.

and in a few the length of the radius actually decreased, although the amount of reduction was within the limits of accuracy of the method of measurement.

As a further control experiment, starfishes of known size were placed in three boxes on a raft in Plymouth Sound on 13 December 1946.

Six *A. rubens* were placed in box R together with six *Tellina crassa*, three *Raphia rhomboides* and one *Venus casina*. Each starfish measured $R = 6 \text{ cm.} \pm 0.1$. No further food was added and the box was left undisturbed until 21 May 1948 when it contained: three *Asterias rubens* ($R = 6.4, 6.2$, and 6.2 cm.), eight *Ciona intestinalis*, four *Ascidella aspersa*, two *Polycirrus caliendrum*, and numerous *Jassa falcata*, as well as the empty shells of the original molluscs. Besides the latter, it is probable that the three surviving starfishes had eaten the remains of the three which had died, as well as possible spatfalls of barnacles.

Boxes L and C each started with six *Asterias rubens* of the same size as in box R, but without any food. When opened on 21 May 1948 they contained:

Box L

Three *A. rubens* ($R = 5.8, 5.7, 5.0 \text{ cm.}$)
Two colonies *Leucosolenia* sp.
Numerous *Jassa falcata*

Box C

Three *A. rubens* ($R = 6.1, 5.1, 3.8 \text{ cm.}$)
Four *Molgula tubifera*
Three *Sycon coronatum*
Three colonies *Leucosolenia* sp.
Two colonies *Halichondria panicea*
Numerous *Jassa falcata* and one empty *Mytilus edulis* shell (2.3 cm. long)

In these boxes the surviving starfishes would again have had the remains of the dead starfishes to feed on, as well as possible spatfalls. In box C the *Mytilus* had also almost certainly been eaten by one of the starfishes.

In all three boxes the amount of food available was infinitesimal in comparison with the long period of the experiment ($17\frac{1}{4}$ months). The starfishes were, therefore, to all intents without food during the greater part of this period and, as the measurements show, there was no significant growth. All the starfishes which survived were emaciated and darker in colour than at the outset of the experiment. In the three individuals which showed a significant decrease in size the arrangement of the spines on the aboral side and of the ambulacral plates suggested a marked contraction of the muscles between the various skeletal plates. This apparent contraction may have been due to actual desorption of muscle tissue, and further observations are being made to check this explanation.

Lack of food therefore stops growth, as would be expected, but this cessation of growth is not necessarily followed by the death of the animal, since it has been shown that starfishes will live for at least 17 months with practically no food. This means that it is not possible to tell the age of a starfish from its size, and a starfish 1 year old may, in fact, measure anything between about 1 and 9 cm. in radius.

Criteria of Breeding

REPRODUCTION

Three main phases may be recognized in the reproduction of a marine invertebrate:

- (a) Maturing of the gametes in the parent gonad.
- (b) Spawning of the gametes, usually directly into the sea, and fertilization.
- (c) Development of the fertilized egg into the adult, usually with an intermediate free-swimming larval stage.

With *Asterias rubens* reliable observations on the reproductive period have been largely based on records of larvae in different localities. Examination of these records shows that there is considerable variation from year to year in the period at which larvae were taken, even in the same locality. There is, however, no certain way of knowing from which local population the larvae have been derived, as they may be carried away from the area in which they were spawned by the action of currents. Collections of larvae have often been taken sporadically and not regularly throughout the year, so that the absence of a record during any period may only mean that no collections were made. As an exception to this criticism mention should be made of the valuable observations on the occurrence of *A. rubens* and other echinoderm larvae in the Sound between Denmark and Sweden recorded by Thorson (1946).

The mechanism of spawning (phase *b*) has been studied in echinoids by Fox (1924) and Palmer (1937). In *A. rubens* Gemmill (1914) found that spawning may be induced by the presence of sperms and ova, but he did not separate ova from sperm when they were used as stimuli to spawning.

The present work is primarily concerned with phase *a*, the process of gonad ripening within wild populations, as distinct from the cytology of gamete maturation—which has been described for *A. rubens* by Gemmill (1914). Data on this process in a number of separated populations may give information on the factors controlling the differences in productivity of the bottom fauna of different areas. Regular examinations were made of the state of the gonads in the parent starfishes.

The relation between body size in *A. rubens* and the size of the gonads varies greatly according to the time of the year. After the breeding season the gonads are thin, short and shrunken caeca, almost never exceeding 2–3 cm. in length, even in the largest starfish. During the period of maturity, on the other hand, the gonads are very large and may extend from their origin near the interradial angle almost to the tip of the arm.

Although this increase is very largely one of volume, the coelomic cavity of the arms in which the maturing gonads are at liberty to grow is essentially elongated, and it has been found most practicable to denote gonad size by length measurements. This method of gonad measurement also allows a direct comparison to be made between gonad size and the size of the parent animal expressed in terms of radius length.

Stages of Ovarian Maturity

The gonads of all the starfishes taken in the hauls were examined living, and records were kept of the state of sexual maturity. To allow comparison of the gonad states between one catch and the next an arbitrary scheme of stages of ovarian maturity was used. This was not attempted in the male, where any separation of stages beyond 'unripe', 'ripe' and 'spawned' was found to be unreliable. For the ovaries six stages of maturity were defined, primarily in terms of the sizes of the oocytes and eggs, but account was also taken of the outer appearance and length of each ovary. Examination of the colour and texture only does not provide a reliable criterion of the stage of sexual maturity reached.

The six stages of ovarian maturity were defined as follows:

1. *Very immature*. Ovary transparent and thin, with a length usually between 0.1 and 0.5 cm. Few early transparent oocytes, with no trace of yolk, up to 40μ in diameter. Most ovaries in this stage were probably virgin.

2. *Immature*. Ovary opaque; length usually between 0.5 and 1.5 cm. Oocytes still transparent, without yolk, but more numerous and up to 80μ in diameter. This stage included many virgin starfishes, but also probably a few which had bred before.

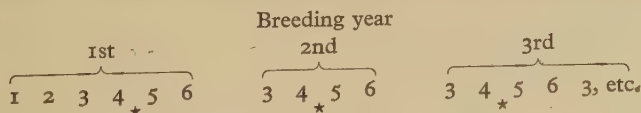
3. *Ripening*. Ovary always opaque, white to yellowish, and more than 1 cm. in length. Distinguished at once from stage 2 by the very numerous oocytes, all yolky, and varying in diameter between 200μ and the diameter of the ripe eggs.

4. *Ripe*. Ovary almost translucent and greatly enlarged with swollen caeca, and nearly always longer than 1.5 cm. The maximum length of the ripe ovary varies considerably, but is commonly between one-tenth and two-fifths of the radius length, sometimes up to seven-eighths of this length. Containing 90% or over of ripe eggs.

5. *Spawned*. Ovary opaque and yellow with shrunken caeca. Usually between 1 and 4 cm. in length, according to the size of the animal. A few oocytes appear in a smear, but the distinguishing character is the residue of a few ripe but unspawned eggs which are in process of breaking up, their yolky material being ingested by amoebocytes.

6. *Spawned and Re-ripening*. Ovary similar in shape and size to that in stage 5, but no unspawned eggs remain, and a fresh generation of yolky oocytes has appeared. This stage occurs in late summer and can be recognized with some certainty up to September. After this it is not distinguishable from stage 3 and so from 1 October all records of this type of ovary with yolky oocytes are recorded as stage 3.

The sequence of stages in the life of an individual starfish appears, therefore, to be



In each year spawning is indicated by an asterisk. Starfishes which have once bred never appear to pass through stage 1 again, although it is possible that a few may return to stage 2. The available evidence shows, however, that after spawning a population never shows any significant increase in the number of individuals in ovarian stage 2. In a few individual starfish the ovaries may show signs of complete atrophy as opposed to the normal seasonal regression.

Analysis of Reproductive Cycles

Rame-Eddystone Grounds. The percentages in each stage of ovarian maturity in 1947 are plotted graphically against time in Fig. 3A. Although each point in this graph is based on a relatively small number of females (owing to the small catches in this area), it is quite evident that the number of females which actually reached sexual maturity (stage 4) during 1947 was surprisingly small. Ripe ovaries were, in fact, only found in the two April catches of this year, and then only in 17 and 19% of the females. This small proportion of ripe females is reflected later in the season in the small percentages of stage 5 recorded. Fig. 3A also shows the large and steady percentages of stages 1 and 2 during 1947. The peak values for stages 1 and 2 in June and July 1947 are probably due to the arrival in the catches of young starfishes which the trawl had previously failed to capture but which had by then reached a catchable size. It is unlikely that these young starfishes had bred before, but they would probably have done so in the following year (1948), that is when they were 2 years old. As their ovaries start to mature in preparation for this breeding the values for stages 1 and 2 should fall off and stage 3 should increase. This is beginning to happen in September and October 1947.

During 1947, therefore, less than 20% of the total female population of starfishes (over $R=3$ cm.) on these grounds produced ripe eggs.

In 1948 comparable samples from the same grounds showed a similar breeding cycle, but with important modifications (Fig. 4A). The most noticeable difference was the greater length of time during which ripe eggs were recorded in 1948, namely February till the beginning of June, with peak egg production in April and May. In 1948, however, the percentage of definitely non-breeding starfishes (stages 1 and 2) was still high, being approximately 40% compared with 50–70% in 1947.

The Outer Grounds. On these grounds the observations on state of maturity showed an entirely different picture. The percentages in each stage of ovarian maturity in 1947 and 1948 are plotted graphically against time in Figs. 3B and 4B. Nearly all the catches from this area were large, the majority totalling over fifty individuals and some over 100. Furthermore, the proportion of females in these catches was nearly always above 50% and so the samples on which Figs. 3B and 4B are based are relatively larger than those which form the basis of Figs. 3A and 4A. Fig. 3B shows that ripe females

were already present (11%) in the population on 7 March, the date of the first catch from this area. The percentage of ripe females increased from then onwards to a peak in the second half of April. On 23 May 1947 there were no

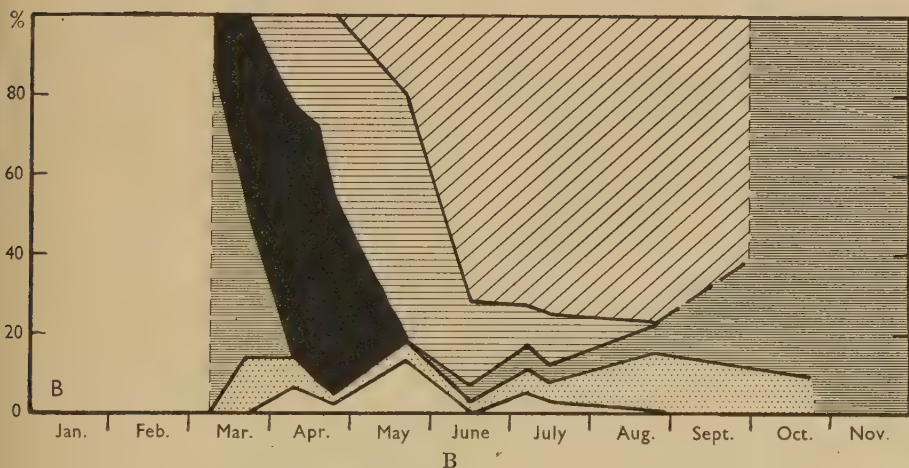
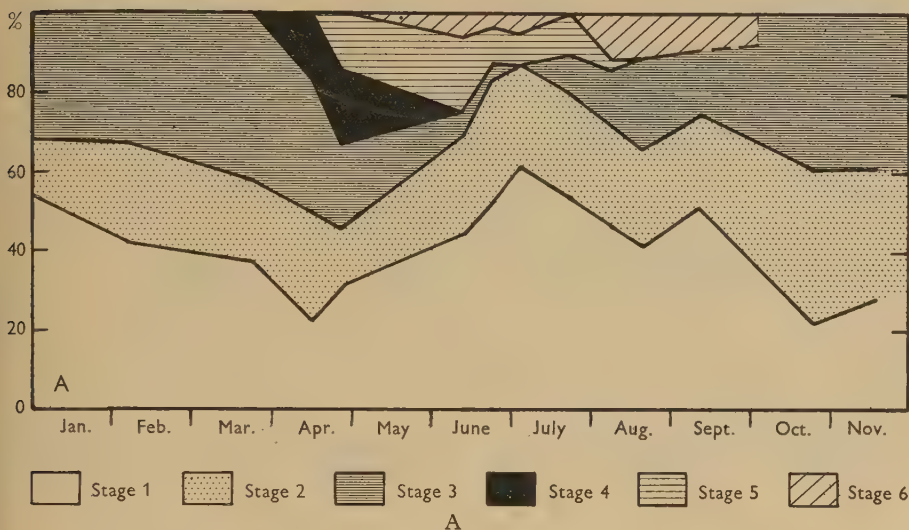


Fig. 3. Ovarian maturity. Percentages in each stage during 1947. A, Rame-Eddystone Grounds; B, Outer Grounds.

ripe females in the population sample. Stage 5 females were dominant in the population in May and the first half of June. After this 'recently spawned' ovaries were again scarce, as they gave place to those in stage 6.

In this area the proportions of stages 1 and 2 combined are remarkably constant and never exceeded 15% of the total population of females.

During 1948 the reproductive cycle (Fig. 4*b*) was essentially similar to that of 1947. Data are, however, available for the early part of 1948, and they show that ripe eggs were produced from February till the end of May with a peak in March and April.

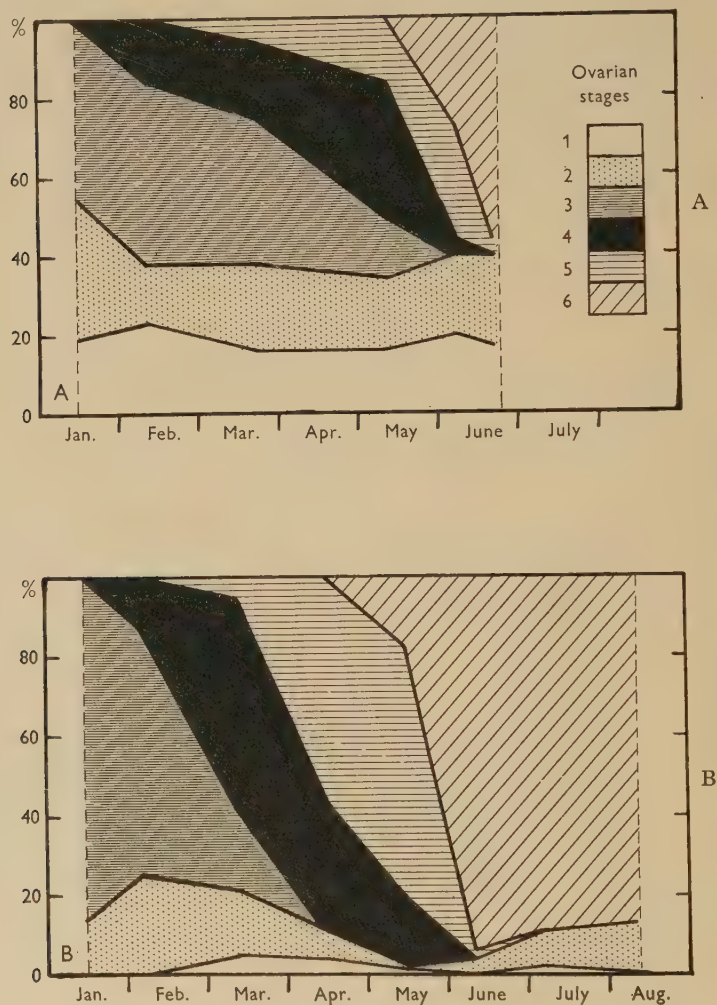


Fig. 4. Ovarian maturity. Percentages in each stage during 1948. A, Rame-Eddystone Grounds; B, Outer Grounds.

On the Outer Grounds the data for both 1947 and 1948 show that the proportions of stages 1 and 2 combined are very constant and only once (early 1948) exceeded 20% of the total population of ovaries.

The Population near E 1. By the time samples were obtained in the area the majority of individuals had already spawned; this is clear from Table VI, which suggests that the peak of the spawning period in 1947 had taken place in May, and so probably a little later than in the Outer Grounds population.

The Cawsand Bay Population. Only one haul was obtained from this area (on 23 May 1947), and as already mentioned the starfishes were all very small and almost certainly belonged to the 1946 brood. In spite of their small size eight of the ten females had already spawned (stage 5), with ripe eggs still present in some tubules. Also two of the eight males were still ripe with motile sperms, and two others showed signs of having spawned recently.

The Plymouth Sound Population. The characteristics of the reproductive cycle in this population were as homogeneous as the size composition. On 10 February 1948 fourteen females were taken, of which one had ovaries in stage 2 and thirteen in stage 3. On 16 April forty-eight females were caught and all were ripe (stage 4).

The Rame Mud Population. In the single sample of ninety-five starfishes from this area only seventeen could be sexed, and of these only five were females, all with ripe gonads. Breeding in this area was evidently very intermittent.

RELATION BETWEEN OVARIAN MATURITY AND BODY SIZE

The criterion of ovarian maturity has been used as an index of the potential breeding efficiency of a number of populations and certain conclusions may now be drawn. Of the two populations most extensively studied that on the Outer Grounds showed a significantly higher percentage of ripe ovaries than the Rame-Eddystone Grounds population. At first sight it might appear that this difference in percentage of females matured between the Rame-Eddystone and the Outer Grounds populations was related to body size, namely that the larger individuals matured and the smaller ones did not. This might explain the differences in maturing between the large-sized and the medium-sized populations, but it would not account for the high percentage of maturity in the small-sized Cawsand Bay population. Nor would it account for the difference in maturity between the Rame-Eddystone population and the somewhat smaller-sized Plymouth Sound population. On 16 April 1948 the Plymouth Sound female starfishes had a mean radius length of 9.5 cm. and 100% of the females had ripe ovaries. In the Rame-Eddystone population at the peak of the breeding season (as determined by the percentage ovarian maturity, 11 May 1948) only 34% of the females were ripe, and yet the starfishes in this sample were somewhat larger (mean $R = 10.5$ cm.) than those in Plymouth Sound.

Furthermore, analysis of the sizes of the mature females in the Rame-Eddystone and Outer Grounds populations provides interesting data. The size distributions of the female starfishes in stages 4 and 5 from the Rame-

Eddystone sample for 28 April 1947 and from the Outer Grounds sample for 25 April 1947 are shown in Table VI. This shows that the size classes $R=6$ cm. and $R=9-13$ cm. were represented in both samples.

TABLE VI. NUMBER OF FEMALES IN STAGES 4 OR 5 IN EQUAL-SIZED STARFISHES FROM TWO POPULATIONS

Grounds and date		Size class in cm.															
		5	6	7	8	9	10	11	12	13	14	15	16	17	18		
Rame-Eddystone (28. iv. 47)	Total ♀♀	1	4	6	10	6	4	5	2	4	0	0	0	0	0		
	♀♀ in stages 4 or 5	1	1	0	1	3	2	2	2	2	0	0	0	0	0		
Outer Grounds (25. iv. 47)	Total ♀♀	0	1	0	0	1	2	5	8	16	13	16	25	12	6		
	♀♀ in stages 4 or 5	0	0	0	0	1	1	5	7	15	11	14	23	11	6		

Analysis of the numbers of stages 4 and 5 in these common size classes shows that: Rame-Eddystone Grounds had twelve in breeding condition out of twenty-five (48%); Outer Grounds had twenty-nine in breeding condition out of thirty-three (88%).

Similarly, comparison of the common size classes in the other pair of contemporaneous breeding-season samples shows that: Rame-Eddystone Grounds (16 April 1947) had two in breeding condition out of seven; and Outer Grounds (18 April 1947) had ten in breeding condition out of eleven.

It appears, therefore, from a comparison of the Outer Grounds and the Rame-Eddystone Grounds populations, that there was a marked difference in the incidence of ripe and spawned ovaries among equal-sized starfishes on these grounds, over 85% of the Outer Grounds female starfishes having reached breeding condition, while on the Rame-Eddystone Grounds under 50% had reached this stage.

The length of the season during which ripe eggs were present was no longer in the Rame Eddystone Grounds than in the Outer Grounds, so that there is no lengthening of the breeding season to account for the low percentage of ripe females on the dates on which samples were taken. Indeed, during 1947, the ripe-egg season in the Rame-Eddystone Grounds was considerably shorter than in the Outer Grounds.

OVARY LENGTHS AND RELATIVE EGG PRODUCTION

The previous analysis gives an index of the number of individuals reaching stages 4-5, but gives no indication of any difference in the scale of gamete production between equal-staged starfishes in different populations. A further analysis of the lengths of the ripe ovaries (stage 4) in equal-sized starfishes from contemporaneous samples is shown graphically in Fig. 5. This shows that in equal-sized starfishes in April 1947 ripe ovaries were longer in the Outer Grounds than they were in the Rame-Eddystone Grounds and,

similarly, they were significantly longer in April 1948 in the Plymouth Sound population than in the early May 1948 sample from the Rame-Eddystone

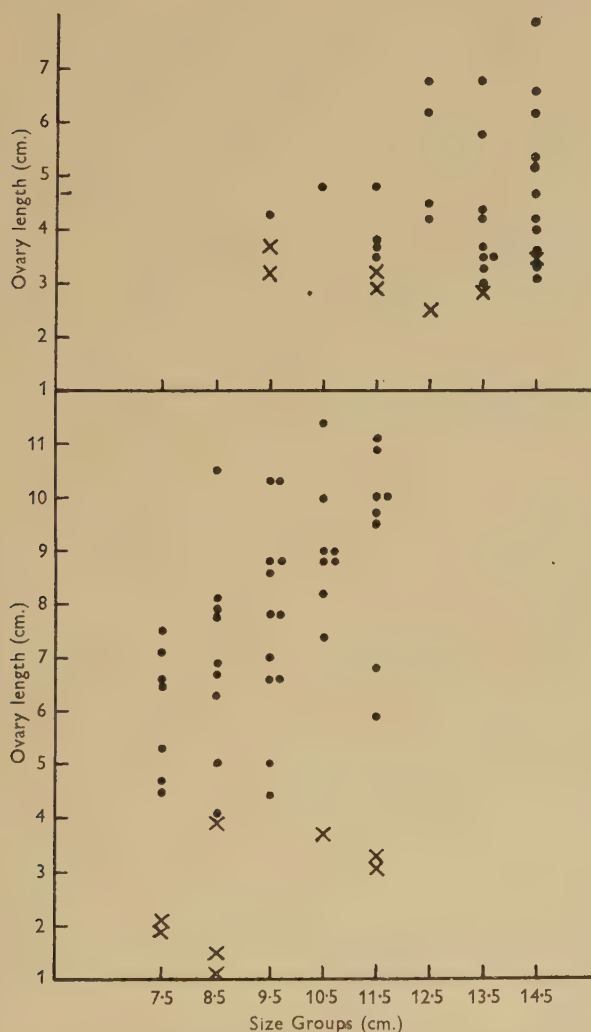


Fig. 5. Lengths of ovaries in stage-4 starfishes in different populations. Above: x, Rame-Eddystone Grounds on 16 and 28 April 1947; •, Outer Grounds on 9, 18 and 25 April 1947. Below: x, Rame-Eddystone Grounds on 11 May 1948; •, Plymouth Sound on 16 April 1948.

Grounds. The production of eggs in the Outer Grounds and Plymouth Sound populations must therefore have been considerably greater than in the Rame-Eddystone Grounds population.

It is interesting to note that in April 1948 the ovaries from the Plymouth Sound sample were sometimes longer, when dissected out, than the starfish arms in which they had been growing. This was due to a certain amount of longitudinal folding of these ovaries within the coelomic cavity of the arms.

DISCUSSION

Study of a number of separate populations of *Asterias rubens* has shown that there is considerable variation in the total productivity on the different grounds. For the two main populations investigated, data were collected over two breeding seasons and they show conclusively that the size means and ranges of the samples from one area and their percentage matured were significantly higher than those from the other area. No attempt has yet been made to assess the absolute or relative numbers of starfishes in these areas, although comparably caught samples from the Outer Grounds were in general larger than those from the Rame-Eddystone Grounds. Some explanation is, however, necessary to account for the differences in growth and maturing of these populations and of those from the other areas which were studied in less detail.

There is no indication of a direct correlation between good growth and maturing and temperature. The 'successful' populations (Outer Grounds, E 1, and Plymouth Sound) were found at opposite extremes of the very small temperature range for any one season. Harvey (1928) found that winter bottom temperatures in 1924 at E 1 (south of the Outer Grounds) were about 10°C ., whereas at L 4 (Rame-Eddystone Grounds) they were approximately 9.8°C ., and 9.0°C . in Plymouth Sound. In summer, however, this relationship was reversed (August, 12.5°C . at E 1, and 13.5°C . at L 4). With minor modifications this relationship has held good in subsequent years. Similarly, with salinity, 'successful' populations were found in both the least polluted waters (Outer Grounds and E 1) and in the most polluted waters (Plymouth Sound), whereas the poorer populations were living in the intermediate waters.

It is considered that the direct factor responsible for the differences noticed is the amount of available food. During the period of the investigations the Outer Grounds and the Plymouth Sound area were very rich in food animals suitable for starfishes. In the Outer Grounds the flat sandy bottom carried a large population of *Chlamys opercularis*, which formed the chief starfish food, as well as a smaller population of *Cyprina islandica*, which is eaten by large specimens of *Asterias* sp. (Hunt, 1925). In the Asia Grounds where the rich Plymouth Sound starfish population was found, the trawl brought up many medium and large *Mytilus edulis*. On the other hand, in the Rame-Eddystone Grounds it is difficult to name any one main food source for the starfishes living there. Trawl and dredge hauls brought up a few *Chlamys opercularis*, and a few tubicolous worms, as well as large clusters of hydroids and bryozoans. In these clusters there were small crabs, lamelli-

branches and other starfishes, but little that could serve as a main food supply for medium and large starfishes. The same may be said of the Rame Mud area, where the epifauna is even poorer, although the infauna, which is largely inaccessible to *Asterias*, is relatively abundant.

The abundance of the supply of *Mytilus* in Plymouth Sound in 1948 was probably the result of an exceptionally good spatfall correlated with the presence of detritus brought down by the rivers Plym, Tamar and Tavy and by the Plymouth City effluents, all of which flow into the Sound; in addition plankton would be brought in from the open sea. A heavy spatfall of *Mytilus* coinciding in time and space with a rich settlement of *Asterias rubens* will provide ideal conditions for the growth of a large starfish population, such as that investigated in Plymouth Sound in 1948. On the other hand, large numbers of young starfishes settling on a bed of adult mussels would not thrive, since their size would be out of phase with that of the food animal. There must, therefore, be a rather limited optimum mean size and total concentration of the food animal before a large homogeneous population of starfishes can be produced. These conditions have been fulfilled on Asia Grounds, but not on the Rame-Eddystone Grounds or on the Rame Mud.

For the Outer Grounds population a different food animal is involved, and whereas a heavy spatfall of *Mytilus* in Plymouth Sound is apparently rare, it is probable that good spatfalls of *Chlamys* are quite usual in the waters of the English Channel. The ultimate factors responsible for the distribution of *Chlamys* are not known, although it is possible that, as they are active swimmers, they may move away from areas poor in food and congregate in more favourable waters. At the same time they are known actively to avoid concentrations of *Asterias rubens*, which will in their turn follow the *Chlamys*. The distribution of *Chlamys* on the sea bottom is, therefore, probably a resultant of both these biological factors. Whereas the Plymouth Sound population, feeding on an abundant fixed food animal, was itself strictly localized in distribution, the Outer Grounds population feeding on a mobile food animal was probably moving to and fro on the sea bottom in pursuit of *Chlamys*. Furthermore, as the *Chlamys* move about, neighbouring groups of *Asterias* will be attracted to the fringes of the Outer Grounds. If this type of dilution of the population occurs, it would account for the wide size ranges of some of the Outer Grounds samples and the dispersion of their means (Fig. 1). There is no evidence for regarding these movements of *Asterias* and *Chlamys* as large-scale migrations involving long distances.

There is no sharp limiting boundary between the Rame-Eddystone and the Outer Grounds populations, although, in practice, the 30-fathom line has been regarded as a convenient line of demarcation, and it is probable that starfishes from the Rame-Eddystone Grounds play a part in the dilution of the Outer Grounds population. On the basis of the growth-rate observations it is likely that many Outer Grounds starfishes had metamorphosed there and had reached

medium size ($R = ca. 6-10$ cm.) and breeding condition in one year. On the other hand, other starfishes of similar sizes caught on the same grounds were probably immigrants, aged 2 or even 3 years, from the Rame-Eddystone Grounds and other neighbouring areas.

There is, unfortunately, no method of determining age in *Asterias*. However, investigation of different wild populations coupled with growth-rate observations have shown that the productivity of a starfish population, as measured by the percentage of matured gonads and by the sizes of these gonads, is not primarily correlated with age. Poorly fed populations will survive and show minimum growth and little or no gonad maturing, whereas well fed populations will grow fast and reach breeding condition within one year from metamorphosis.

SUMMARY

Considerable differences were found in the size compositions of populations of *Asterias rubens* off Plymouth. These differences were not correlated with age.

Laboratory observations on rate of growth showed that well fed starfishes grow fast during summer and autumn and somewhat slower in winter. Poorly fed starfishes did not increase in size, but were able to survive for long periods with a minimum of food.

In favourable conditions *A. rubens* may grow to a radius size of 8-9 cm. in one year and may also reach breeding condition during this time.

Investigation of breeding cycles by determination of the percentage of females in different stages of ovarian maturity showed further differences between populations. Starfish populations with a high percentage of large and ripe ovaries during the breeding season were not necessarily those with large body-size means.

It is considered that the differences in size composition and production of ripe eggs were primarily correlated with food, and observations are given on the food animals in the areas supporting 'successful' starfish populations.

For the production of a large homogeneous starfish population it is necessary for spat to fall on an area rich in suitable food animals. There is an optimum relationship between size of starfish and size of food animal which must be maintained if the starfish population is to remain large and homogeneous and show maximum productivity during the breeding season.

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THE FAUNA OF SAND AND MUD BANKS NEAR THE MOUTH OF THE EXE ESTUARY

By N. A. Holme, B.A.

From the Plymouth Laboratory

(Plates I and II and Text-figs. I-II)

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INTRODUCTION

In 1901 Allen & Todd (1902) made a survey of the fauna of the Exe Estuary consisting of collections of the macrofauna of the intertidal sand and mud-banks, and some trawling and dredging. An account of the Foraminifera of the estuary is given by Worth (1902). Since 1901, considerable changes have occurred in the physiography of the lower part of the estuary, and the present paper records some observations made on the fauna in the area most affected by these changes.

The papers by Allen & Todd (1900, 1902) on the Salcombe and Exe Estuaries are almost the first comprehensive estuarine surveys. Since about

1928 a number of more detailed surveys have been published, some of which deal with the quantitative aspects of populations in sand- and mud-banks. One of the most recent of these is that by Spooner & Moore (1940) on the macrofauna of the intertidal muds of the Tamar estuary. Serventy's (1934) survey of the Scolt Head Island fauna and Beanland's (1940) work on the Dovey estuary are accounts of the fauna of sand- and mud-banks in sheltered and near-marine conditions, comparable to those described in this paper.

Populations on sandy and muddy shores have been described by Stephen (1929*a*), Elmhirst (1931), Pirrie, Bruce & Moore (1932), Rees (1939), Watkin (1942), and Brady (1943). Besides these general surveys, there have been more intensive studies of certain species, such as those of Stephen (1928, 1929*a, b*, 1931, 1932) on the biology of *Tellina tenuis* and certain other lamellibranchs.

Most surveys have necessarily been restricted to collections made during a limited period, and little is known of changes in the populations from season to season or from year to year. Fischer-Piette (1931) found a correlation between salinity changes in the estuary of La Rance and the up-river penetration of certain animals in successive seasons and years, but his observations were primarily on non-burrowing species.

It is well known that both salinity and the type of soil influence the distribution of species within an estuary; but the exact role of each and the influence of other factors is still virtually unknown. Some light on the causes of distribution is revealed from the work of Day & Wilson (1934) and Wilson (1937, 1948), on the influence of particular grades of sand on the metamorphosis of certain polychaete larvae. The larvae show a tendency to settle on soil characteristic of the adult habitat, and, as *Ophelia bicornis* from the Exe, may postpone metamorphosis until a suitable grade of sand has been reached.

As a result of erosion of Dawlish Warren an area of sand has come to lie in close proximity to, and grading into, the original mud-banks. Thus it was possible to study the fauna over a wide range of soils, without the complications which usually occur due to differences in salinity, currents or wave action.

ACKNOWLEDGEMENTS

I am indebted to the Trustees of the Balfour Fund for a grant to meet collecting expenses, and to the Deputy Provincial Director of the Ministry of Agriculture and Fisheries at Starcross for the provision of accommodation while collecting was in progress. I am also grateful to the Soils Department of the above establishment for their help with the pH readings, and in other ways. Much of the collecting equipment was kindly lent by the Director of the Plymouth Laboratory.

I am especially indebted to Dr C. F. A. Pantin, F.R.S., for his help, both as Administrator of the Balfour Fund, and for his encouragement and advice

In planning the course of the work. The collecting and the sorting of specimens at Starcross was only made possible by the generous help of the following: Miss U. M. Grigg, Miss S. M. Davies, and Messrs B. O. C. Gardiner, D. Langridge, R. M. Laws, A. J. Lee, A. W. Mansfield and H. Swift. Mr and Mrs G. M. Spooner were also of great assistance for a few days at the beginning of the summer. Mr A. J. Lee, who was surveying the Warren, has kindly provided an up-to-date map of the area which is reproduced, with modifications, in this paper.

The following have been of great assistance in the techniques of measuring physical conditions: Dr H. W. Harvey, F.R.S., Dr C. H. Mortimer and Dr J. A. Ramsay.

The later stages of this work and the writing of this paper were made during the term of a D.S.I.R. training grant at the Plymouth Laboratory. I am indebted to the Director and Staff of the Plymouth Laboratory for advice and assistance during this period.

Certain salinity readings were kindly supplied by the Ministry of Agriculture and Fisheries, Fisheries Experimental Station, Castle Bank, Conway.

The following have been kind enough to identify or check certain groups: *Nemertinea*—Dr J. E. Smith; *Annelida*—Mr D. P. Wilson; *Mollusca*—Dr V. Fretter, Miss S. M. Davies, Miss U. M. Grigg, Mr R. Winckworth; *Crustacea*—Dr E. E. Watkin, Mr G. M. Spooner, Mrs W. M. Tattersall; *Pisces (Ammodytes)*—Mr P. G. Corbin; *Zostera* spp.—Mr T. G. Tutin; *Algae*—Dr M. Parke.

I am indebted to Mr F. S. Russell, F.R.S. and Dr T. J. Hart for helpful criticism of the manuscript.

THE EXE ESTUARY

The River Exe is tidal up to Countess Wear, 9 miles from the mouth, but between Countess Wear and Topsham the channel is fairly narrow and the water is almost fresh. Between Topsham and Exmouth the estuary is about a mile wide and is 6 miles long. A small river, the Clyst, enters the estuary near Topsham and a few streams flow into the estuary at various points. At high tide the estuary is almost completely covered by water, but at low tide extensive sand- and mud-banks are uncovered through which a shallow main channel winds. Near Exmouth the estuary narrows, being diverted at right angles to the east by a sand spit on the western shore, called Dawlish Warren. The channel runs parallel to Exmouth shore for 2 miles, being separated from the sea at low tide by a large sand-bank known as Pole Sands. The banks in the upper part of the estuary are of mud, but nearer Exmouth they become more sandy. Two banks of clean sand occur near the mouth: Bull Hill Bank and Pole Sands. The river channel is well scoured and has a bed of stones in the lower part of the estuary.

Tidal streams are very swift, particularly near the mouth. Opposite Exmouth Dock a speed of 5 knots (9.25 km./hr.) may be reached on spring tides. The scour produced by the currents causes banks opposite the main channel to slope down steeply near low-water mark. Thus most of the banks are at high- and mid-tide levels, and very little additional area is uncovered at low spring as compared with low neap tides. The tidal range is 12.2 ft. (3.72 m.) at spring tides, and 4.8 ft. (1.46 m.) at neap tides.

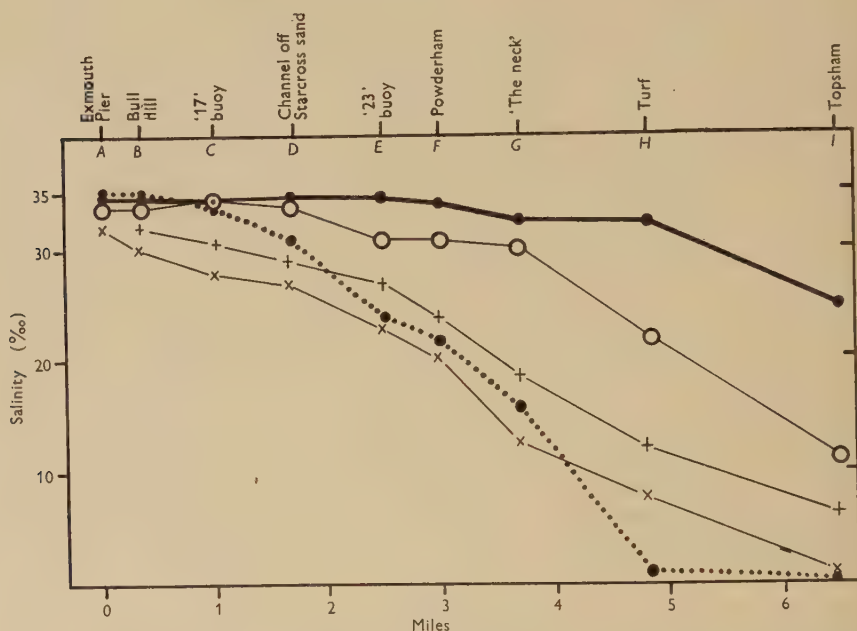


Fig. 1. Surface salinities in the Exe Estuary. Distances are measured up the main channel from Exmouth Pier. The area studied in this paper is opposite the station marked 'Bull Hill'. Samples were taken on the following occasions: —●—, high spring tide (12 ft. 5 in.), 3. ix. 47; —○—, high neap tide (9 ft. 6 in.), 27. vii. 47; —+—, low neap tide (10 ft. 2 in.), 28. viii. 47; —×—, low spring tide (12 ft. 2 in.), 18. vii. 47; ····, high neap tide (10 ft. 2 in.), 2. iii. 48.

A certain amount of sand is mixed with all the deposits; and in dry windy weather sand may be blown up the estuary from Dawlish Warren, so adding to the sand-content of the banks.

The considerable width of the estuary enables small waves to be formed within it, and in addition swell from the sea may be felt as far up as Starcross at high tide. During a recent south-east gale the sea was sufficiently rough inside the estuary to damage severely the railway embankment below Starcross.

Sewage from Exeter is discharged into the river near Countess Wear, and sewers empty into the estuary opposite the villages and towns on its shores. There is no chemical pollution.

The extent of the fresh-water inflow was discussed by Allen & Todd (1902). The watershed area of the Exe is 584 square miles (1512 km.²) and it was found that conditions at Exmouth were almost marine, whereas at Topsham fresh water was recorded at low tide after heavy rain. Some additional salinity records are given in this paper. They were made by running a motor-boat at top speed up the estuary, taking surface water samples at intervals. Starting about half an hour before high or low tide it was possible to take most of the samples during the period of slack water. Samples were taken at high and low spring and neap tides in the summer of 1947, and one set of samples was taken in March 1948. The results are summarized in Table IX and Fig. 1. In the lower part of the estuary conditions are marine at high tide, but salinity drops to about 30‰ at low tide. The greatest range of salinity occurs at about Turf, 1½ miles below Topsham, and the river is evidently brackish for a short distance above Topsham.

It seems likely, however, that few estuarine species are subjected to such extremes of salinity. At low tide the greater part of each bank is uncovered, and so not exposed to the lowest salinities. In addition, Reid (1930) has shown that a stream of fresh water flowing over intertidal sand has little effect on the salinity of the water retained in the sand, which presumably is of about the mean of the various salinities to which the bank is subjected. Species with an 'open' burrow, such as *Arenicola* will, however, be exposed to the salinity of the overlying water rather than to that of the surrounding sand.

The fauna of buoys is exposed to the surrounding water at all times, but Milne (1940) has shown that mussels close their valves when the salinity drops below 25‰, the water retained in the shell at low tide being of higher salinity than that of the water outside.

The main channel is shallow for the greater part of its length. This, and the ease with which the water may be disturbed by waves and currents, renders it unlikely that any marked stratification of water layers of different salinities would occur. Some records made in connexion with the Ministry of Agriculture and Fisheries' Mussel-Washing Station at Lymptone show, however, that stratification may occur under certain conditions:

(a) *In calm weather* (25 September 1917)

Neap tides. High water 12 noon. Wind S., light. Samples in channel off Powderham Bathouse (half-way up the estuary).

5.12 p.m.	Density at surface	1.009
5.15 p.m.	Density at bottom (9 ft.)	1.023
5.20 p.m.	Density at bottom (9 ft.)	1.021
5.25 p.m.	Density at surface	1.005

(b) During floods (18 January 1918)

High tide 10.19 a.m. Water very high, due to floods and melting snow. Winds S.W., fresh. In channel between Starcross and Lymptone.

12.15 p.m.	Density at surface	1.002
12.15 p.m.	Density at 6 ft. depth	1.015
12.20 p.m.	Density at 8 ft. depth	1.021
12.20 p.m.	Density at 5 ft. depth	1.004
12.23 p.m.	Density at 6 ft. depth	1.017
12.25 p.m.	Density at 7 ft. depth	1.020
12.27 p.m.	Density at surface	1.002

Clearly fresh water was flowing out over the denser salt water, the line dividing the two water masses being at a depth of 5-6 ft. The surface samples were muddy, while the bottom water samples were clear.

DAWLISH WARREN

The Warren is a spit jutting out across the mouth of the Exe, and formerly narrowing it to a channel a quarter of a mile wide between Warren Point and Exmouth (see Fig. 2). It consists of two separate spits: the Outer and Inner Warren. The Outer Warren is a line of sand-dunes on the seaward side of the Inner Warren; it was (in 1939) about $1\frac{1}{2}$ miles long, its north-eastern end forming an area known as Warren Point, on which were a number of bungalows. The Outer Warren has been subject to considerable erosion in recent years, and Warren Point has now disappeared.

Between the Inner and Outer Warren is a low area with little vegetation known as Greenland Lake. This was formerly flooded at high spring tides, but its connexion with the sea has now been closed by a barricade. It is, however, still liable to occasional flooding, and this presumably prevents the establishment of permanent vegetation.

The Inner Warren is an established spit, with a heath-like appearance, and a few small trees. The soil is sandy, and it is used as a golf course. This spit was rather shorter than the Outer Warren and has until recently been completely protected by the latter on its seaward side.

A survey of the Warren made by Mr A. J. Lee showed that the Inner Warren is founded upon a bed of clay rising above high-water mark. On the seaward side the clay dips down steeply and has not been found under the Outer Warren. On the northern shore of the Warren the clay is visible on the surface in places, and forms a gently sloping layer under the mud flats for some distance from it.

These observations confirm the suggestion made by Worth (1902) that the western end of the Warren is a genuine spit of land, whereas the eastern end and the Pole Sands are due to littoral drift.

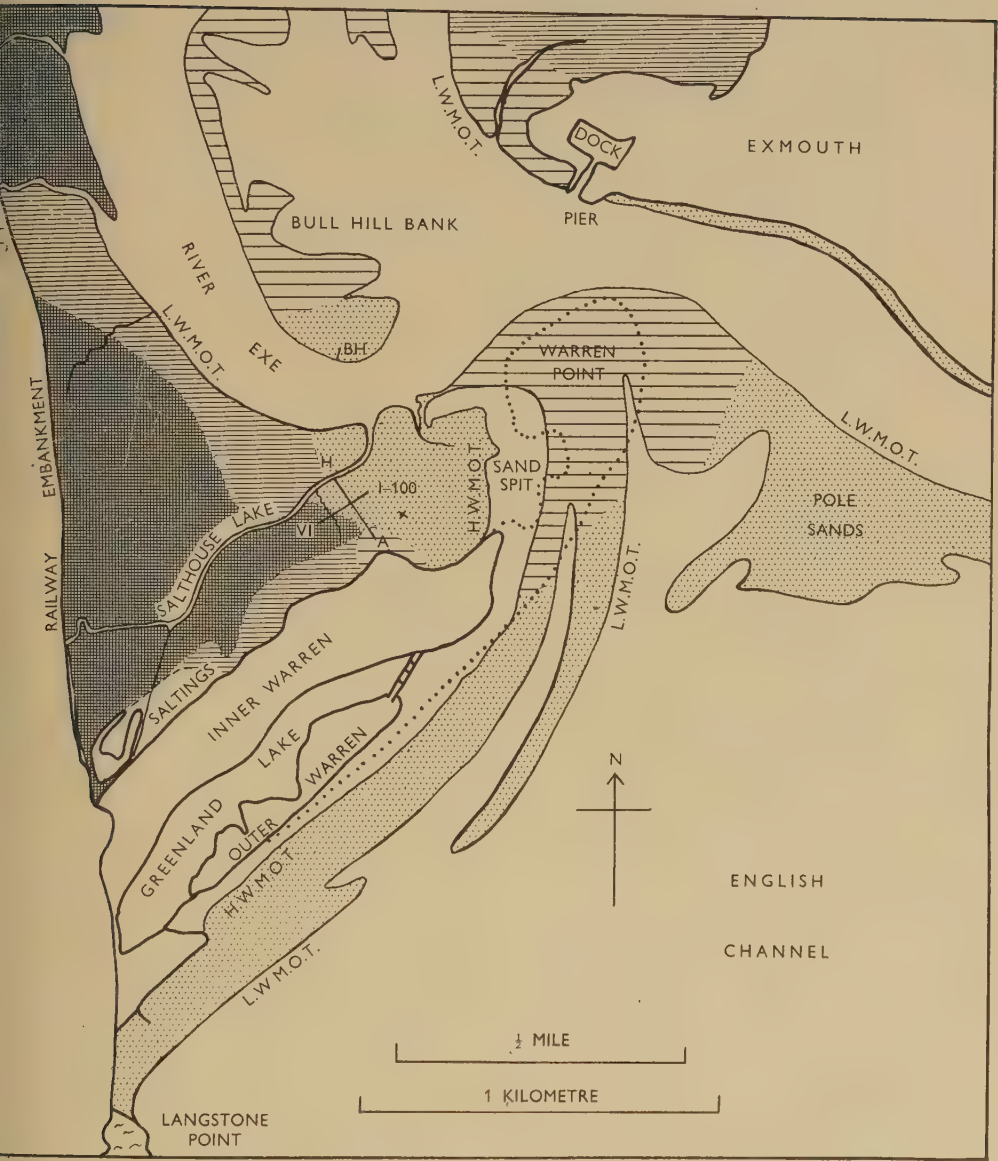


Fig. 2. Map of the lower part of the Exe Estuary, from a survey by A. J. Lee, July 1947. The position of the traverses is indicated. Note that erosion has nearly doubled the high-tide channel opposite Exmouth.

- Mud. ▨ Muddy sand. ▩ Sand. ▤ Gravel.
- Outline of Warren Point in 1935

EROSION OF DAWLISH WARREN

Little is known of the extent of the Warren before the eighteenth century; records for 1723 give its area in that year as 398 acres. Since then the Warren has been slowly reduced in size by attrition along its seaward face. In 1888 the area was only 191 acres. In 1859 and 1869 breaches were made in the line of dunes forming the Outer Warren, but these were subsequently closed. By about 1943 the width had been reduced to such an extent that a breach was made through the narrow neck joining Warren Point to the remainder of the Outer Warren. A channel about 50 yards wide was formed through the spit, the bottom of the channel being rather below half-tide mark. Between 1943 and 1946 Warren Point was reduced to a sand bank by the action of waves and currents. In October 1946 the breach was closed by littoral drift, and the end of the Outer Warren now consists of a hooked sand spit over which the sea occasionally washes during storms. The high-water channel opposite Exmouth has been widened to 600 yards. At low tide the remains of Warren Point are uncovered. Stages in erosion may be seen in the aerial photographs reproduced in Pls. I and II (p. 232).

Although the Warren has been diminishing in width for a long time, it was not until the length of the spit had decreased that any effects within the estuary were noticeable. Wave action near the mouth of the estuary has increased, but this chiefly affects Bull Hill, a bank already well scoured by currents.

Before the recent changes occurred the tidal range at Topsham, at the northern end of the estuary, was the same as at Exmouth at neap tides, and only a few inches less at spring tides. Hence the increase in width at its narrowest part could have no effect on tidal heights within the estuary. During south-easterly gales, however, water accumulates in the estuary more than previously, and there is an increasing danger to the railway embankment in consequence.

Since tidal heights and fresh-water inflow are unchanged, salinity conditions cannot have altered appreciably.

The main biological effect of erosion has been through the redistribution of sand within the estuary. Sand has been washed and blown up the estuary in a north-westerly direction from Warren Point. The sand has come to lie in a belt extending up to Cockwood, and may be responsible for a decline in the productivity of the cockle beds there. The sand has become mingled with the mud in most places, but just inside Warren Point there is a stretch of newly deposited clean sand. Two hundred yards to the west is an area of mud covered with *Zostera*. In the intermediate zone a range of soil types, from sand to mud, is found.

SCOPE OF THE SURVEY

Since 1902 there has been little published work on the estuary. Crawford (1937*c*) recorded certain Crustacea from the estuary; and Beanland (1940)

considered that the absence of *Corophium volutator* from an area in which it had been found by Allen & Todd was due to decreasing shelter resulting from erosion of the Warren.

The area selected for study lies between Dawlish Warren and a small stream running parallel to it through the mud flats, known as Salthouse Lake. Allen & Todd (1902) did not collect here, but they gave a list of species from a similar ground at a slightly lower level to the north of the stream.

In all, collections were made on three traverses: (i) along a traverse passing from sand to mud, stations all being at about half-tide level; (ii) on an intertidal traverse in the same region, passing from high- to low-water marks, in which most stations were on sand; (iii) a short traverse across the top and edge of Bull Hill Bank.

METHODS

Faunistic collections

Collections were made of a $\frac{1}{4}$ m.² surface area dug to a depth of about 10 in. The area to be dug was marked out by a square metal frame of side half a metre and depth 6 in., which was driven into the ground. This prevented collapse of soil into the hole during digging.

The soil was sieved through a gauze sieve with holes 1 mm. square. A 'souping' technique, as used by Spooner & Moore (1940), was adopted in the muddier areas. Practically all the soil passed through the sieve at most stations, but *Zostera* and other plant remains were often abundant in the sievings. Now and then a sieve with round holes 0.8 mm. across was also used, but never on the top 2-3 in. of soil where small individuals chiefly congregate. Occasionally, mainly in the *Zostera* areas, sub-sampling was resorted to after the larger specimens had been picked out.

'Sievings' were taken back to Starcross, where they were sorted and preserved, with preliminary identifications. All specimens were kept and have been identified and size-grouped by the author while at Plymouth.

The collecting technique seems adequate for all the larger specimens, but it is likely that only a fraction of the smaller worms, etc., were retained by the sieve. With animals of a definite shape and size, such as the Gastropod *Hydrobia ulvae*, a constant lowest size of animal is retained by the sieve; but the proportion of other small specimens must largely depend on the duration and violence of sieving: in time all would pass through. At least one moderate-sized worm (*Scoloplos armiger*?) has a habit of actively crawling through the meshes of the sieve and so tends to be lost.

In so far as no animals below 1 mm. were included, this survey of the populations is incomplete. But the study of the micro- and meio-benthos requires special techniques outside the scope of this work. A sieve with mesh of 1 mm. is about the smallest that can conveniently be used for sieving a large bulk of sand, and for subsequent sorting without resorting to a lens.

Along each traverse stations were at 100 ft. (30·48 m.) intervals; at each two collections were made 3 ft. on either side of the station along the line of the traverse. These were designated as +3 and -3 ft. from each station.

Intermediate stations were also worked and are designated by the distance in feet from the preceding station. Thus Station II+33 was 33 ft. from Station II and 67 ft. from Station III. Stations were I-100, I, II, III, IV, V and VI on the main traverse, and A, B, C, D, E, F, G and H on the intertidal traverse. These traverses cross at Stations II and E, which are therefore identical. Stations on Bull Hill were measured in feet from a point 'BH' at the top of the steep slope of the bank.

Population figures from adjacent collections at each main station are given separately to emphasize the variation to be expected due to patchy distribution of certain species.

Physical conditions

Salinity was measured in two ways:

(i) Titration with silver nitrate solution using potassium dichromate as indicator. Comparison was made by titration of a sea-water sample taken at sea outside the estuary. This was assumed to have a salinity of 35·0 ‰ as no accurate salinity determinations were made.

(ii) Using a brass and also a glass hydrometer with density ranges from fresh to salt water. These instruments give an approximate reading only, to which a temperature correction must be applied.

pH. The pH of marine soils seems to be chiefly related to the carbon dioxide concentration (Dr H. W. Harvey: personal communication), and since determinations were not made in the field it is difficult to assess the importance of this factor. The pH of the water in the soil was determined by comparing samples, obtained by digging a small hole in the soil and allowing it to fill with water, with standard buffer tubes, using cresol red as indicator.

pH was also measured electrically. A glass jar was filled full of soil, and from the middle of this sample a small quantity was taken out for pH measurement, which was determined within 24 hr. of collection. The soil was mixed to a smooth paste with the minimum quantity of sea water, and the pH of the mixture measured.

Temperature. Readings of soil temperatures were made by inserting a thermometer into a small hole in the ground made with a stick. Temperatures were recorded with the bulb at $\frac{1}{2}$ in. and at 3 in. depths below the surface.

Water table. A small hole dug in the soil was allowed to fill with water. The top of the water is approximately equal to the level of the water table.

Tidal levels. A number of stations were levelled to Ordnance Datum by means of a 'Dumpy Level' and a bench-mark on Dawlish Warren. Tidal heights are given relative to Chart Datum, which is 0·2 ft. below M.L.W.M.S.T.

Soil analysis. Grade analysis was carried out by means of the standard method used in agriculture. This method has been applied with success to

soils on the shore by Beanland (1940) and Watkin (1942). It is not in itself sufficiently precise to distinguish the slight differences in soil grade which seem to affect the distribution of certain species. If material retained on the standard 0.2 mm. sieve is passed through a series of sieves of slightly coarser mesh a more exact grading of the sand can be achieved.

Owing to difficulty in obtaining a Standard 70 I.M.M. (0.2 mm.) sieve, a sieve of 80 meshes to the inch was substituted. This had openings 0.22 mm. across. Results obtained with this sieve have been compared with those made with a standard sieve (Table X). Many of the grains were about 0.2 mm. in size so that there is some divergence in results from those made with the standard sieve. In the present investigation the following grades were distinguished:

Stones and fine gravel	Retained on 2 mm. sieve
Very coarse sand	Retained on 0.5 mm. sieve
Coarse sand	Retained on 0.256 mm. sieve
Medium sand	Retained on 0.22 mm. sieve
Fine sand	0.22-0.02 mm.; passing 0.22 mm. sieve and settling in 5 min.
Silt and clay	Less than 0.02 mm.; still in suspension after 5 min.

The method used is based on that described by Piper (1942):

Samples were taken from the top 4 in. of soil and were air-dried.

The soil was graded through a 2 mm. sieve, all retained on the sieve being rejected. 10 g. of soil were weighed out and were treated with hydrogen peroxide in the cold, and subsequently at 100° C.

Hydrochloric acid was added to dissolve carbonates.

Water was added until the depth in the beaker was 10 cm.; this was allowed to stand and the liquid decanted off. This was repeated.

The small quantity of silt decanted off was allowed to settle, and was dried and weighed.

The soil was dispersed by rubbing with a rubber pestle, and was washed through a 0.22 mm. sieve.

The sand retained on the sieve was dried and rubbed on the sieve until no more passed. Sand passing through was added to that in the beaker.

The residue on the sieve was graded through 0.5 and 0.256 mm. sieves.

The material in the beaker was filled up to 10 cm. depth with water and caustic soda solution was added. After stirring it was allowed to settle for 5 min. (at 18° C.). The silt was decanted off.

Successive decantations were made, a small quantity of concentrated ammonia solution being added each time. This was repeated until the liquid was clear after 5 min.

The silt was allowed to settle in a large jar, and was dried and weighed. To this weight was added that obtained from decantation from acid solution.

The residue after decantation was fine sand.

Soil grades have been expressed as percentages of their total weight, not of the original 10 g. of soil. There is a small loss in weight during analysis, mainly due to solution of carbonates. For brevity the silt-plus-clay content of a soil has here been referred to as its silt content.

It is suggested that for marine soils the solution of carbonates is unnecessary, and may give a misleading result where large quantities of shell-fragments are present; but in most of these samples the calcium carbonate content was fairly low.

Nomenclature

Nomenclature is that of the Plymouth Marine Fauna (Marine Biological Assoc., 1931), but with the following alterations and additions:

- Eteone longa* (Fabricius). See Fauvel (1923).
Ophelia bicornis Savigny. See Fauvel (1927).
Spiophanes bombyx (Claparède). See Fauvel (1927).
Bathyporeia pilosa Lindström, and *B. sarsi* Watkin. See Watkin (1938).
Urothoe grimaldii Chevreux. See Chevreux & Fage (1925).
Corophium arenarium Crawford. See Crawford (1937a).

Algae. Nomenclature in accordance with *A Handbook of the British Seaweeds* by Newton (1931).

Flowering plants are named in accordance with the *Handbook of the British Flora* by G. Bentham, revised by Sir J. D. Hooker, seventh edition, 1924. The reference to *Zostera hornemanniana* Tutin is in Tutin (1936).

The spelling of place-names follows the Ordnance Survey: the names 'Bull Hill' and 'Pole Sands' being used in preference to Allen & Todd's 'Bullhill' and 'Polesands'.

DESCRIPTION OF THE TRAVERSES

The Main Traverse

Conditions

Seven main stations at 100 ft. intervals were worked; at each two collections were made from $\frac{1}{4}$ m.² Some collections at intermediate positions were also made.

The general appearance of the traverse may be summarized as:

I-100 → I	Well-drained clean sand
I → I + 70	Moist clean sand
I + 70 → III - 10	Muddy sand with small pools. <i>Arenicola</i> casts numerous
III - 10 → III + 11½	Shallow stream running over sand
III + 11½ → III + 57	Sand becoming muddier
III + 57 → III + 88	Soft mud with some sand
III + 88 → IV + 12	Soft mud with patches of <i>Enteromorpha</i>
IV + 12 → IV + 87	Clayey mud
IV + 63 → IV + 67	Narrow stream
IV + 87 → VI	Mud with <i>Zostera</i> spp.

(All descriptions are of the conditions at low tide.)

Analyses of the soil grades are given in Table I. The silt content rose gradually from 0.7% at I-100 to 2.2% at II+67. Beyond Station III there was a sharp rise, with a maximum of 22.6% at Station V. The small quantity of silt at Station III was probably due to the stream over the sand at this point. The proportions of the coarser grades are constant along the traverse; in all

but one or two samples the greatest proportion consisted of 'fine sand' (0.22-0.02 mm.). Over 95 % of the total was made up of grades below 0.5 mm.

TABLE I. SOIL GRADES ON THE MAIN TRAVERSE, EXPRESSED AS PERCENTAGES BY WEIGHT

The dimensions are those of the sieves used.

Station	> 2 mm.	2-0.5 mm.	0.5-0.256 mm.	0.256-0.22 mm.	0.22-0.02 mm.	Silt and clay
I-100	Few stones	4.6	26.6	23.9	44.2	0.7
I-40	Very few stones	0.5	9.3	12.3	77.5	0.3
I	Nil	2.8	22.2	23.2	51.7	0.05
I+8	Nil	1.4	17.2	25.3	56.0	0.35
I+33	Nil	1.6	17.8	25.0	55.0	0.7
I+67	Nil	1.2	19.9	29.1	49.2	0.7
II	Nil	1.1	13.9	21.2	62.2	1.6
II+33	Nil	0.7	9.4	15.9	72.6	1.35
II+67	Nil	0.8	10.8	16.5	69.7	2.2
III	Nil	1.7	10.4	15.8	70.7	1.5
III+33	Nil	1.1	3.2	6.0	82.7	6.9
III+67	Nil	0.7	6.2	7.9	76.8	8.4
IV	Nil	0.2	2.7	3.3	77.3	16.6
IV+33	Nil	0.6	7.5	8.9	73.6	9.4
IV+67	Nil	0.6	5.5	5.1	73.8	15.0
V	Nil	0.8	4.7	3.0	68.9	22.6
VI	Few shell fragments	6.8	18.0	10.4	53.8	11.2

The traverse was situated at about half-tide mark, but sloped upwards towards Stations I and I-100 which were a little below mean high-water mark of neap tides. These stations were not covered at extreme neap tides. Stations III, IV, V and VI were at about the same level (Fig. 3).

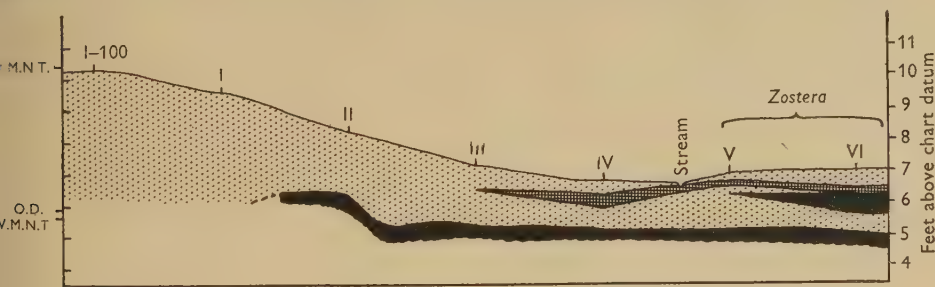


Fig. 3. Profile of the main traverse. The distance between stations is 100 ft., and the vertical scale is greatly exaggerated. The white area is below the depth investigated.

Mud or sand.
 Shell-layer.
 Clay.

Much of the traverse lay on top of a bed of clay, which was quite near the surface at Stations V and VI. In addition, Stations III-VI inclusive overlay a bed of shell remains at a depth of about a foot. The shells were of the same species as those now living in this area, consisting mainly of *Hydrobia*, *Cardium*, *Scrobicularia* and *Macoma*.

The greater height of the bank at Stations I and I-100 was presumably due to deposition of sand from Warren Point in this area. It was not possible to find any trace of the original surface of the bank, and it was presumed that the new sand had become mingled with the old layer. The depth to which the bank had been inundated was, however, determined by the discovery of a wood post in the sand. (Position marked by a cross in Fig. 2.) This post had been driven into a bed of clay on the original bank and was half covered by sand. On it were found empty shells of *Balanus* sp. and *Chthalmus stellatus* at a maximum depth of 26 in. below the surface of the sand. The post appeared fairly new and had probably been erected within the past 10 years. The lower end of the post was embedded in clay, and it seemed unlikely that it had been disturbed since its original erection. Thus sand had probably accumulated here to a depth of about 30 in. The traverse area is clearly at the edge of the region covered by sand, and Station I-100 had probably been covered by about 2 ft. of sand, and Station I and possibly also Station II, to a lesser depth.

The nature of the banks before the recent changes is uncertain. The Ordnance Survey Map of 1903-4 marks the area inside Warren Point as 'mud', whereas that of 1935 marks it as 'sand and mud'. It had probably become more sandy as the Outer Warren narrowed, being finally inundated by clean sand about 1943 when the breach occurred.

Currents in the Salthouse Lake area were slight, but there was some scour in the bed of the stream at low tide. There seemed to be no significant differences in current action along the traverse. Mud stirred up by waves and currents may tend to settle in the sandy areas of the traverse, and the present condition of these banks can only be temporary. Wave action in this area is normally negligible.

pH measurements showed no significant differences along the traverse.

(i) Interstitial water		pH
12. vii. 47, low tide	Station I	7.8
	Station II	7.8-8.0
	Station III	8.0
(ii) pH determined electrically		
6. viii. 47, low tide	Station II	7.3
	Station IV	8.3
	Station VI	7.8
14. viii. 47, low tide	Station I	7.5
	Station II	7.5
	Station III	7.9
	Station IV	7.9
	Station V	7.5

Salinity and temperature. Miscellaneous salinity records showed that the salinity in the area was near-marine, there being no differences along the traverse (except, perhaps, during rain). On 11 July 1947 (high tide 11.15 a.m.,

eight 9 ft. 6 in.) the surface salinity of water covering certain stations was measured:

Station	Salinity (‰)	Depth of water (in.)	Time (p.m.)
I	34	4	12.20
III	34	24	1.00
VI	34	15	1.15

On 2 days, at spring and neap tides, all-day readings of conditions were made:

19 August 1947. High tide: 8.37 a.m. 13 ft. 2 in. (spring tide); 8.45 p.m. 13 ft. 2 in. A fine sunny day, but with some haze. Calm sea. Gentle breeze. There had been no rain for the previous fortnight and the River Exe was very low. Records were made of:

(i) The temperature in the soil at each station at depths of $\frac{1}{2}$ and 3 in., when uncovered by the tide.

(ii) The temperature and salinity at Station III, taken in the overlying water at high tide, and in a small pool at low tide.

(iii) Temperature and salinity of the surface water in the main channel by Bull Mill Bank.

(iv) Duration of exposure of each station at low tide.

(v) Depth of the water-table in the soil.

(vi) Air temperature.

The results are summarized in Tables II, III, IV, XI, XII and Figs. 4 and 5.

The readings show:

The surface ($\frac{1}{2}$ in.) soil rose to a high temperature, 26.5° C. being the maximum recorded. The temperatures attained by the different types of soil were very similar.

Thus at 4.15 p.m. the maximum soil temperature was 26° C. and the minimum 25° C.

A temperature gradient is set up in the soil during the day, the temperature at 3 in. depth being about 2° C. lower than in the surface soil. In the evening the soil cools

and the gradient is reversed. At Station III the temperature ranged from 19° C. at high tide to 27.25° C. in a pool at low tide. The temperature changes occurring when

the tide covered this station again in the evening were not as sudden as might be expected, as the water had already been warmed as it flowed over banks in the vicinity.

At low tide the salinity rose from 34.5 to 38 ‰ as a result of evaporation.

Station I was uncovered for over $7\frac{1}{2}$ hr., whereas Stations II–VI were each uncovered for about 6 hr. On a neap tide the relative differences in the periods of emergence would be much greater.

Observations on the water-table showed that it was at the surface at all stations except I–100, I and II. Drainage at Station I was very much more thorough than

at II. The better drainage at this end of the traverse may be due to the nature of the soil, the greater height of these stations, or to the absence of a clay layer at any

significant depth.

In the main channel the temperature ranged from 18.75 to 22.5° ; the highest temperature being at low tide. The salinity showed a corresponding fluctuation, being

35.5 ‰ at high tide, and 32.5 ‰ at low tide. For most of the tidal cycle the salinity was over 34 ‰, there being a marked drop for an hour or two each side of low water.

A set of readings was also taken on 12 August 1947 on a neap tide, results being similar to those above. In addition it was noted that:

The salinity of the water in Salthouse Lake was found to drop to about 19 ‰ for about an hour at low water. The fresh-water inflow of this stream is small, and does not appear to exert any local influence on the fauna.

At Station I the water-table dropped to 13 in. depth, as compared with 11 in. on a spring tide. This increased drainage was probably due to the absence of water flowing down the beach from regions above high neap-tide level. Thus on spring tides the quantity of water draining down from these areas prevents the water-table from dropping as much as on neap tides.

TABLE II. TEMPERATURE READINGS ON THE MAIN TRAVERSE, 19 AUGUST 1947

Temperatures ($^{\circ}\text{C}$) were recorded at depths of $\frac{1}{2}$ and 3 in. below the soil surface. A dash indicates that the station was covered by water.

Time	Air ($^{\circ}$)	I		II		III		IV		V		VI	
		$\frac{1}{2}$ in.	3 in.	$\frac{1}{2}$ in.	3 in.	$\frac{1}{2}$ in.	3 in.	$\frac{1}{2}$ in.	3 in.	$\frac{1}{2}$ in.	3 in.	$\frac{1}{2}$ in.	3 in.
7.30 a.m.	22	—	—	—	—	—	—	—	—	—	—	—	—
8.00	20.25	—	—	—	—	—	—	—	—	—	—	—	—
9.30	20.25	—	—	—	—	—	—	—	—	—	—	—	—
10.00	23	—	—	—	—	—	—	—	—	—	—	—	—
11.00	22.25	—	—	—	—	—	—	—	—	—	—	—	—
12 noon	23.25	24.75	22	24	21.75	—	—	—	—	21.75	20.5	22.25	21
1.05 p.m.	22.5	26	24	25	23	25.5	23.5	25	22.5	25	22.5	25.5	22.5
2.10	22.25	26.5	24.5	26	24	26	24	26	24	26	24	26.25	24
3.15	21.5	25.75	24.75	26	24.5	26.5	25	26.25	25	26	24.5	26.25	24.5
4.15	21.5	25.25	24.5	26	24.75	25.5	25.5	25.5	24.5	25	24	25	24
5.15	21.5	23.5	24	23	23.5	23.5	24	23.5	24	23.25	23.5	23.5	24
6.10	—	23	23	22.5	23	—	—	—	—	—	—	23	23.5
6.35	20	—	—	—	—	—	—	—	—	—	—	—	—

TABLE III. DEPTH OF THE WATER-TABLE BELOW THE SOIL SURFACE, 19 AUGUST 1947

At Stations II+33 to VI the water-table was at the surface at all times. Station I was uncovered at about 11 a.m. and Station II at 11.50 a.m. S, water-table at surface.

Time	I (in.)	I+50 (in.)	II (in.)
11.20 a.m.	S	—	—
11.40	—	S	—
12 noon	S	S	S
1.05 p.m.	S	S	$\frac{1}{2}$
2.20	5	$\frac{1}{4}$	I
3.15	8	I	I
4.10	10	$\frac{3}{4}$	I $\frac{1}{2}$
5.15	10	6 $\frac{1}{2}$	I
6.05	11	6 $\frac{1}{2}$	I

TABLE IV. DURATION OF EXPOSURE AT LOW TIDE OF STATIONS ON MAIN TRAVERSE, 19 AUGUST 1947

Station	Time
I	7 $\frac{1}{2}$ hr. +
II	6 hr. 24 min.
III	c. 6 hr.
IV	5 hr. 50 min.
V	6 hr. 15 min.
VI	6 hr. 17 min.

There are a number of other factors, not readily measurable, which may affect distribution. The oxygen content of the soil cannot be easily determined in the field; the degree of aeration of the soil can, however, be measured by the depth of the 'black-layer'. Bruce (1928) has shown that the black-layer

s produced by ferrous sulphide, which is oxidizable to ferric oxide. The top of the black-layer is a level at which there is equilibrium between sulphide production at a depth in the soil and oxidation in the more superficial layers.

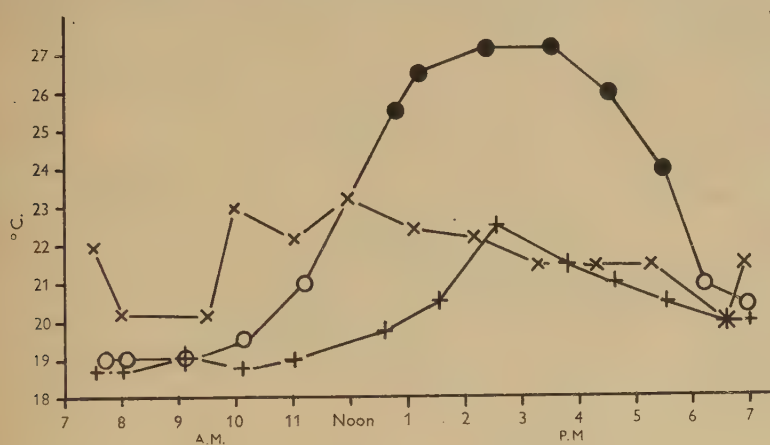


Fig. 4. Temperatures at Station III, and in the channel near Bull Hill, 19. viii. 47. —○—, water covering III; —●—, pool at III (low tide); —×—, air temperature; —+—, main channel.

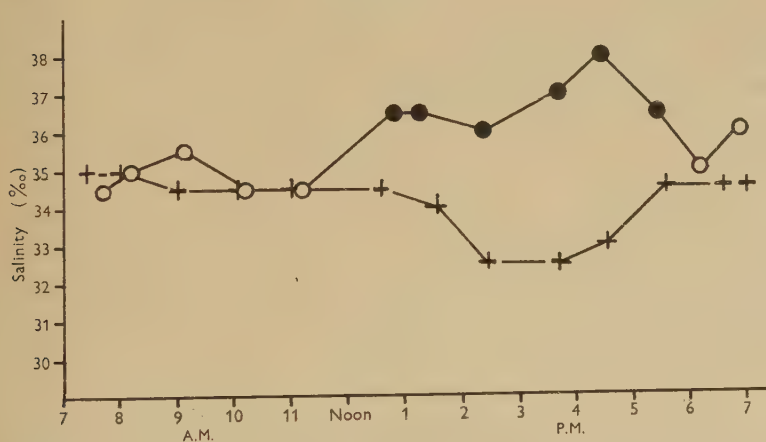


Fig. 5. Salinities at Station III, and in the channel, 19. viii. 47. —○—, water covering III; —●—, pool at III (low tide); —+—, main channel.

The black-layer tends to occur where there is little circulation (of water) through the sand, or where much organic matter occurs. The black-layer was within an inch or so of the surface from Stations II to VI, but was at a greater depth in the well-drained areas. The smell of hydrogen sulphide was not noticeable when any of the muds were disturbed, so that it is unlikely that extremely anaerobic conditions occurred anywhere on the traverse.

There seems to be no satisfactory method of estimating the organic content of marine soils, but it can be assumed that the organic content of the mud covered by *Zostera* was very much higher than elsewhere.

To summarize—the main factors which differed along the traverse were:

- (1) Soil grade, particularly changes in silt content.
- (2) Presence or absence of surface vegetation.
- (3) Organic content of the soil.
- (4) Drainage.
- (5) Oxygen-tension in the soil, as shown by the 'black-layer'. This is related to organic content and soil drainage.

The stations have been shown to be subject to similar conditions of:

- (1) Intertidal height.
- (2) Salinity and other conditions associated with the overlying water—due to the close proximity of the stations.
- (3) Soil temperature (at least in hot weather).
- (4) pH.
- (5) Wave and current action.

Another factor to be considered is the age of the various banks. Stations III–VI inclusive are evidently long established, but sand has recently accumulated at the other stations, and the communities must have developed in the past few years. Thus there is a possibility that succession may be taking place; this can only be established by observations over a number of years. In October 1948 the area was revisited, but no marked changes in the fauna seemed to have occurred since the preceding summer.

Fauna

Results obtained from the quantitative sampling along the traverse are shown in Table V and in Fig. 6.

It will be seen that many species are rather patchily distributed, considerable variations in counts from adjacent stations being experienced. A few species, e.g. *Tellina tenuis* are, however, fairly evenly distributed.

A check on counts of *Arenicola marina* was provided by the density of casts on the surface (Fig. 7). The number of casts of this species per m.² were counted at intervals of 6 ft. along the traverse, corrections being made where one worm appeared to have produced more than one cast. The area was sufficiently calm for casts to persist for several days, and the numbers agreed well with those found in the digging. It would appear that a $\frac{1}{4}$ m.² sample is adequate for assessing the numbers of a comparatively sparse animal such as *Arenicola*.

Collections were made over a period of 2 months (July and August 1947) so that it is possible that some differences were due to seasonal changes. No very great differences are shown, however, between, for example, the fauna

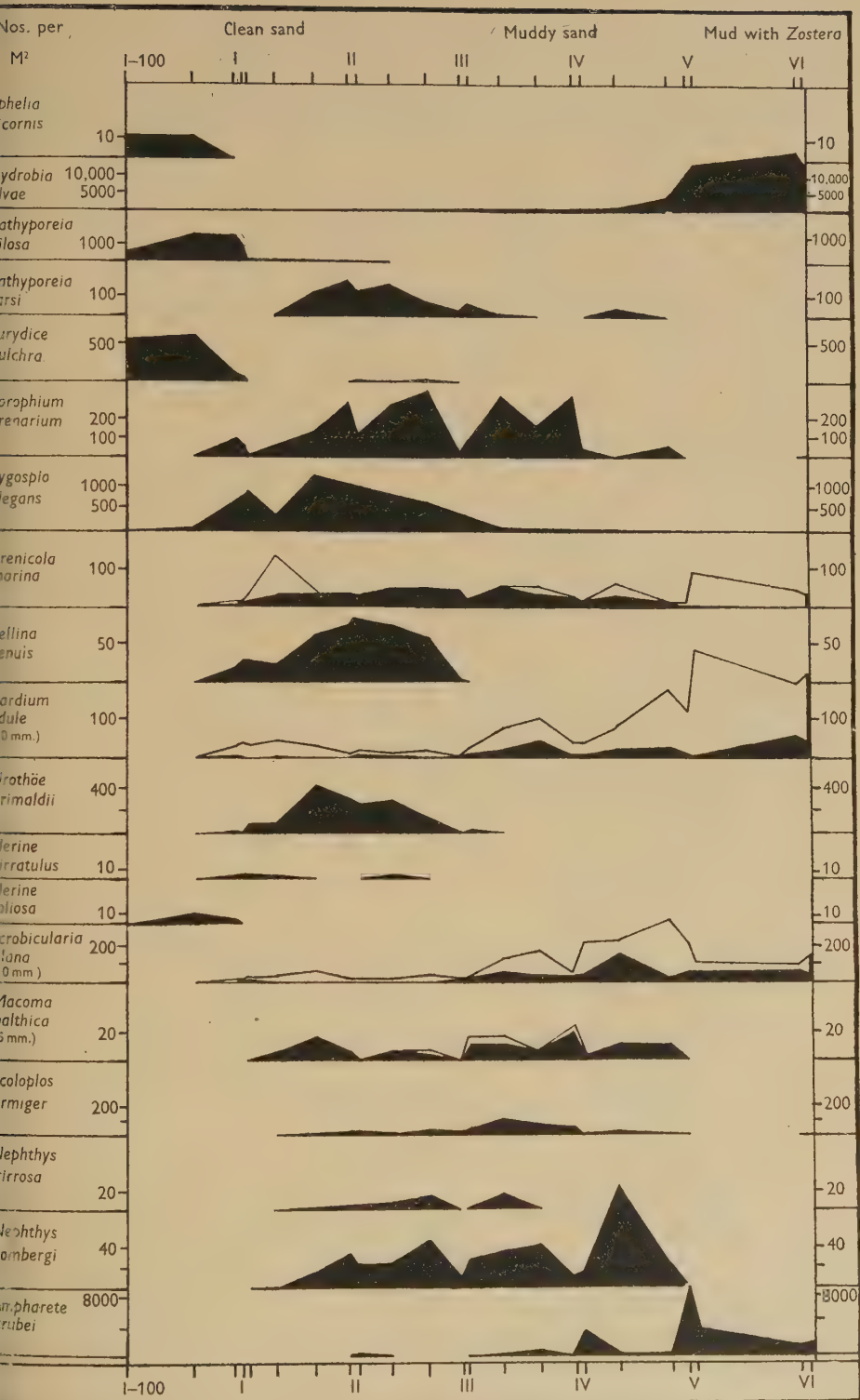


Fig. 6. The distribution of certain species on the main traverse. Small individuals are indicated by the outlined areas; adults by the solid black areas. The figures in brackets under the names of lamellibranchs indicate the length measurement dividing small individuals from adults.

at Station I+3 (collected on 3 July) and of I+8 (collected on 22 August). The main changes likely to have occurred are in the sizes of the animals, as

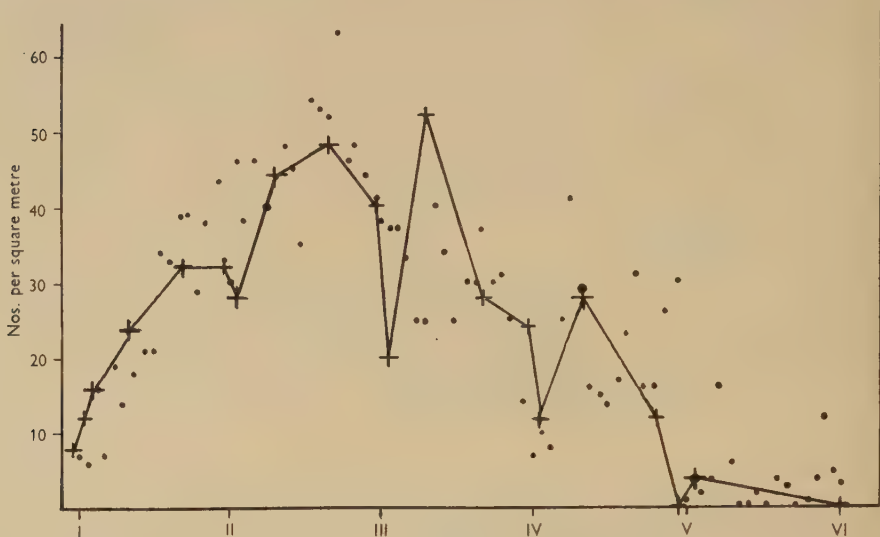


Fig. 7. Comparison of results obtained by counts of casts of adult *Arenicola marina*, and of numbers obtained by digging. ●, numbers of casts; —+—, worms dug up.

TABLE VI. VERTICAL DISTRIBUTION OF SPECIES IN THE SAND AT I+30

Numbers per $\frac{1}{4}$ m.² j, young individuals; +, present.

	0-4 in.	4-8 in.	8-12 in.
<i>Nemertinea</i>	7	I	—
<i>Eteone longa</i>	10	—	—
<i>Nereis diversicolor</i>	I	—	—
<i>Nephtys hombergi</i>	—	I	—
<i>Nerine cirratulus</i>	—	I	—
<i>Pygospio elegans</i>	+	—	I
<i>Spiophanes bombyx</i>	—	2	I
<i>Arenicola marina</i>	26j	2j+5	I
<i>Clitellio ater</i>	85	2	—
Other worms	—	I	—
<i>Bathyporeia pilosa</i>	6	I	—
<i>Urothoe grimaldii</i>	2	20	I
<i>Corophium arenarium</i>	16	—	I
Dipterous larvae	6	—	—
<i>Mytilus edulis</i> spat.	I	—	—
<i>Tellina tenuis</i>	6	—	—
<i>Macoma balthica</i>	2	—	—
<i>Scrobicularia plana</i>	10j	—	—
<i>Cardium edule</i>	11	—	—
<i>Hydrobia ulvae</i>	136	—	—

shown by measurements of the shells of molluscs and in the settlement of larvae. Thus megalopae of *Carcinus maenas* were found in early July, whereas only small metamorphosed individuals were found in late July and in August.

The vertical distribution of species at Station I + 30 is shown in Table VI; it will be seen that practically all species occur in the top 4 in., notable exceptions being *Arenicola marina* and *Urothoe grimaldii*.

The close proximity of the various types of ground may also affect the distribution of certain species. Individuals may stray from their typical habitat (perhaps as a result of 'population pressure') so that in time a species will come to colonize all suitable grounds. This spreading tendency presumably operates continually and will result in a fringing zone where individuals may occur on quite atypical grounds. The extent of this zone will vary with the migratory ability of the species and the degree of unsuitability of the ground to be traversed. The outstanding example here was *Hydrobia ulvae*, normally inhabiting the mud, particularly the *Zostera* beds, but which is continually endeavouring to extend its range so that specimens occur even on the sandy grounds. They would not occur there but for the contiguity of their normal habitat.

The fauna of the main traverse may be arbitrarily divided into a number of zones:

(1) *Fauna of clean loose sand*. Stations I-100 and I-40. The silt content was less than 1% and the grade of sand was coarser than at other stations on this traverse. The sand was very well drained, there being no black-layer near the surface.

Typical species were (Station I-40):

	Per m. ²		Per m. ²
<i>Ophelia bicornis</i>	12	<i>Bathyporeia pilosa</i>	1448
<i>Nerine foliosa</i>	12	<i>Corophium arenarium</i>	16
<i>Pygospio elegans</i>	A few	<i>Hydrobia ulvae</i>	32
<i>Eurydice pulchra</i>	612		

(2) *Fauna of firm moist sand*. Stations I-III. The sand was rather finer than at the previous stations. The silt content rose from 0.05% to a maximum of 2.2% at II + 67. The bank sloped down gently, so that while Stations I to I + 67 were fairly well drained, the subsequent stations had standing water on the surface. A black layer usually occurred within a few inches of the surface.

Typical species were (Station II + 33):

	Per m. ²		Per m. ²
<i>Nephtys hombergi</i>	24	<i>Urothoe grimaldii</i>	268
<i>N. cirrosa</i>	8	<i>Corophium arenarium</i>	280
<i>Scoloplos armiger</i>	12	<i>Tellina tenuis</i>	76
<i>Pygospio elegans</i>	Common	<i>Macoma balthica</i>	8
<i>Arenicola marina</i>	44	<i>Cardium edule</i>	8 young
<i>Bathyporeia sarsi</i>	164	<i>Hydrobia ulvae</i>	448

Ophelia bicornis and *Nerine foliosa* were no longer present, and *Eurydice* was much less frequent. *Bathyporeia pilosa* had been replaced by *B. sarsi*, probably due to the fall in height. According to Watkin (1938) *B. pilosa* is restricted to a narrow zone at about H.W.M.N.T., whereas *B. sarsi* has a wider range extending down to below low-water mark. A number of species appeared at

about Station I and extended almost the length of the traverse; e.g. *Nephtys hombergi*, *Scoloplos armiger*, *Scrobicularia plana* and *Cardium edule*. But *Bathyporeia sarsi*, *Tellina*, *Urothoe* and *Nerine cirratulus* were restricted to the clean sand of this zone.

(3) *Muddy sand*. Stations III+33 to IV+80. This was a transitional zone from sand to mud. At Station III+33 the silt content was 6.9%, and a maximum of 16.6% silt occurred at Station IV. The other grades of soil were in very similar proportions to that found elsewhere in the traverse. The rise in silt content seems to be the cause of the absence of *Bathyporeia*, *Tellina*, *Urothoe* and *Nerine*; but the species extending into this zone usually show a higher density than on the clean sand.

Typical species were (Station IV+3):

	Per m. ²		Per m. ²
<i>Nephtys hombergi</i>	16	<i>Corophium arenarium</i>	44
<i>Glycera convoluta</i>	20	<i>Macoma balthica</i>	4
<i>Pygospio elegans</i>	Present	<i>Scrobicularia plana</i>	180 young and 40 adult
<i>Arenicola marina</i>	12	<i>Cardium edule</i>	8 young and 28 adult
<i>Ampharete grubei</i>	3552	<i>Hydrobia ulvae</i>	620
<i>Melinna palmata</i>	8		

Large numbers of *Ampharete* occur; this species being most abundant where the silt content is high. *Pygospio* occurred in small numbers, and thus inhabits a wide range of soils.

(4) *Mud with Zostera*. Stations V and VI. The soil contained about 10–20% of silt, and was of a rather clayey consistency. When walking over it, one's feet sunk in only a few inches. Holes dug in the mud persisted for months after digging. The surface of the mud was covered by a dense growth of *Z. hornemanniana* Tutin and *Z. nana* Roth, which provided a refuge for numerous small *Carcinus maenas* and *Hydrobia ulvae*. Small specimens of *Arenicola marina* were abundant. The burrowing fauna was, if anything, a little less dense than on the muddy sand. *Macoma*, *Scoloplos* and *Nephtys hombergi* were absent.

Typical species were (Station V+3):

	Per m. ²		Per m. ²
<i>Arenicola marina</i>	88 small and 4 adult	<i>Cardium edule</i>	284 young and 4 adult
<i>Ampharete grubei</i>	3984	<i>Littorina rudis</i>	20
<i>Carcinus maenas</i>	160	<i>L. littorea</i>	84
<i>Scrobicularia plana</i>	48 young and 60 adult	<i>Hydrobia ulvae</i>	13,280

Conditions

The intertidal traverse

This was at right angles to the main traverse, crossing it at Station II, which is identical with Station E. Stations were at 100 ft. intervals and were designated A, B, C ... H. 'A' was near high-water mark, and 'H' at low-water mark. Stations A, B and C were on gravel, with some admixture of sand. The fauna at these stations was imperfectly sampled owing to difficulties in

sieving. From C + 12 to H the soil was fairly clean moist sand, overlying the bed of clay. Grade analyses showed a silt content of under 1% for stations from D downwards (Table VII).

TABLE VII. SOIL GRADES ON THE INTERTIDAL TRAVERSE, EXPRESSED AS PERCENTAGES BY WEIGHT

Station	> 2 mm.	2-0.5 mm.	0.5-0.256 mm.	0.256-0.22 mm.	0.22-0.02 mm.	Silt and clay
A	Many stones	24.3	44.5	19.6	11.1	0.5
B	Few stones	5.7	38.7	29.7	24.0	2.0
C	Few stones	2.5	9.3	10.0	73.8	4.4
D	Nil	1.6	19.5	25.0	53.0	1.0
E	Nil	1.1	13.9	21.2	62.2	1.6
F	Nil	0.8	13.9	26.1	58.7	0.6
G	Nil	0.4	8.4	28.9	61.3	0.9
H	Nil	0.2	4.5	16.5	77.7	1.0

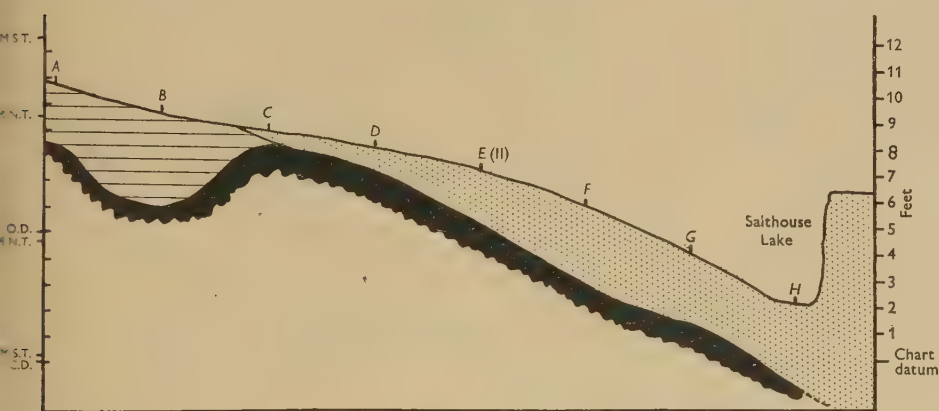


Fig. 8. Profile of the intertidal traverse. Vertical scale greatly exaggerated. Interval between stations is 100 ft. The white area is below the depth investigated.

Sand.
 Gravel.
 Clay.

The profile of the traverse is shown in Fig. 8. The bank sloped down to Salthouse Lake, so that there was little scouring of the banks near low water. This is in contrast to banks adjacent to the main channel which are exposed to a considerable tidal stream. The water-table was at or near the surface at all stations, and a black-layer was usually present at a depth of a few inches. Other conditions were similar to those to which the main traverse was exposed.

pH was determined electrically from samples taken at low tide on 21 August 1947:

	pH		pH
A	7.9	E	7.5
B	7.9	F	7.8
C	7.7	G	7.8
D	7.8	H	8.0

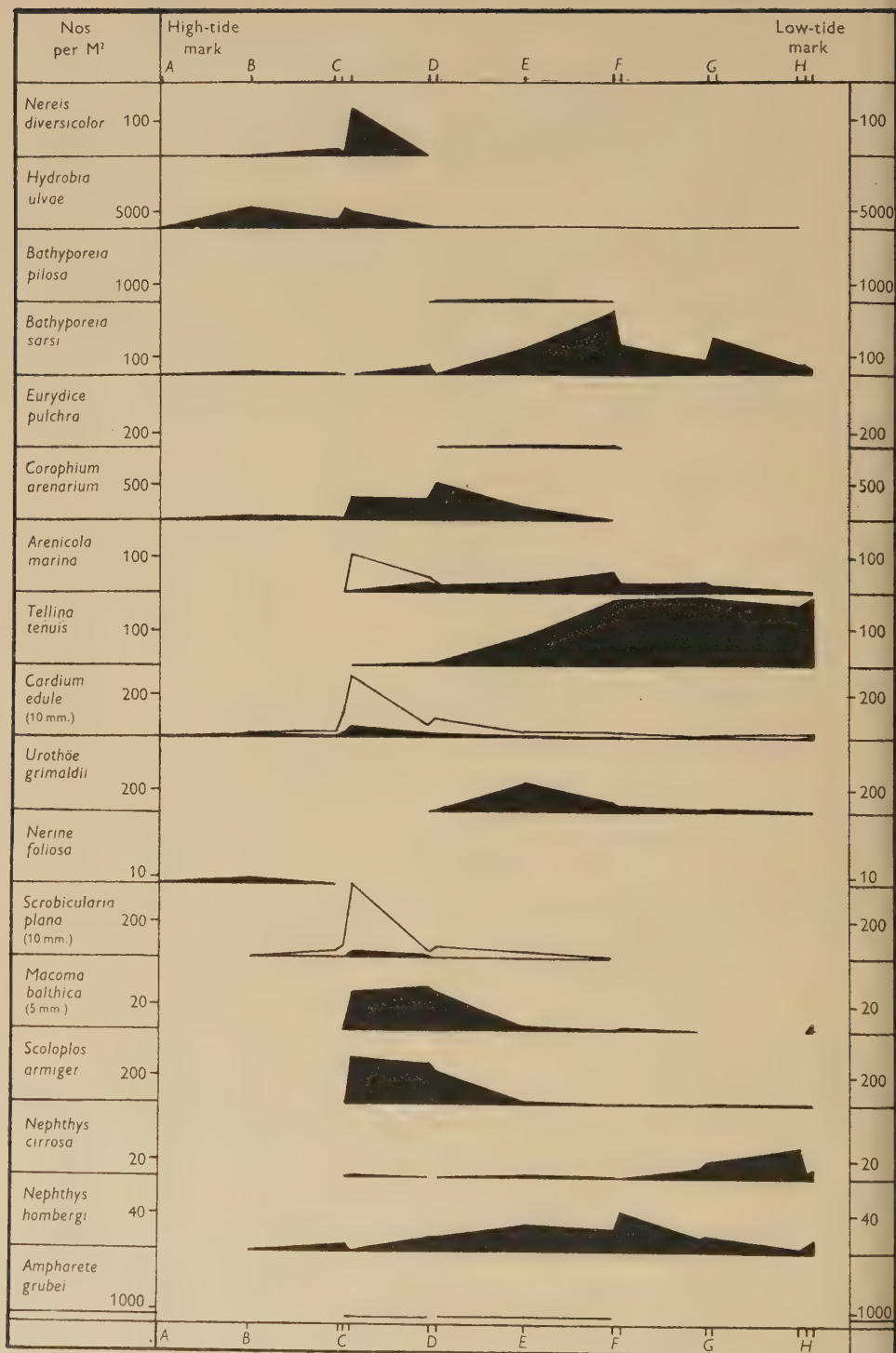


Fig. 9. Distribution of certain species on the intertidal traverse. For explanations see Fig. 6. Station 'E' is the average of numbers from Stations II-3 and II+3.

Fauna

The results obtained from quantitative sampling are shown in Table V and in Fig. 9. Only one collection was made at Stations A and B; and additional collections were made at C+15 and H+15, the latter being in the bed of Salthouse Lake. No other intermediate stations were worked.

The stations are too few to give a detailed picture of the distribution of the fauna, the object of these collections being to determine the intertidal distribution of species occurring in the main traverse. At Stations A, B and C the fauna was poor, especially in burrowing species. At C-3 typical species were:

	Per m. ²		Per m. ²
<i>Nereis diversicolor</i>	20	<i>Cardium edule</i>	8 young and 12 adult
<i>Nephtys hombergi</i>	8	<i>Littorina rudis</i>	4
<i>Corophium arenarium</i>	24	<i>L. littorea</i>	36
Larval Diptera	44	<i>Hydrobia ulvae</i>	2468
<i>Scrobicularia plana</i>	16 young		

At Station C+15, off the edge of the gravel, many species were abundant. The silt content was probably about 3%, but was not determined. Small individuals of *Arenicola*, *Cardium* and *Scrobicularia* were very abundant. Typical species included:

	Per m. ²
<i>Nereis diversicolor</i>	132
<i>Nephtys hombergi</i>	4
<i>Scoloplos armiger</i>	316
<i>Arenicola marina</i>	100 small and 4 adult
<i>Corophium arenarium</i>	312
<i>Mytilus edulis</i>	24 young and 68 adult
<i>Macoma balthica</i>	32
<i>Scrobicularia plana</i>	372 young and 32 adult
<i>Cardium edule</i>	224 young and 52 adult
<i>Hydrobia ulvae</i>	5000

The intertidal distribution of species is discussed on pp. 218-28. It is apparent that most of the species encountered have a fairly wide intertidal range, so that the small differences in height occurring along the main traverse would have little effect on their distribution.

The distribution of the following species may, however, be affected by small changes in height: *Nereis diversicolor* occurred at about H.W.M.N.T., and was consequently scarce on the main traverse, which was at a slightly lower level. *Bathyporeia pilosa*, *Eurydice pulchra* and *Nerine foliosa* occurred only at about half-tide mark, and this may account for their occurrence only at the higher stations on the main traverse. Drainage may also be an important factor in determining their distribution.

Bull Hill Bank

This was a bank of clean sand in the middle of the estuary near Dawlish Warren. The bank was scoured by strong currents, and to a lesser extent by waves; the surface of the sand being consequently furrowed, and the edge

facing the main channel sloped away steeply. The top was at about half-tide mark, and was fairly level.

The sand was rather coarser than that from Salthouse Lake. A sample from the top of the bank (from Station BH + 100) giving on analysis:

(mm.)	(%)	(mm.)	(%)
> 2	—	0.256-0.22	30.1
2-0.5	5.1	0.22-0.02	10.3
0.5-0.256	54.0	Silt and clay	0.5

Independent analyses of the sand from Bull Hill Bank and Salthouse Lake are given by Wilson (1948).

There was no black-layer in the soil, which was very well drained, except near low-water mark, where it remained saturated at low tide.

Salinity and temperature conditions were similar to those in Salthouse Lake.

The fauna was investigated by a single traverse passing through the steep edge of the bank, and for a short distance across the top. A single collection from $\frac{1}{4}$ m.² was made at each station.

TABLE VIII. FAUNA OF BULL HILL BANK

Clean sand at all stations. Numbers per $\frac{1}{4}$ m.²; *j*, young individuals; ' - ' stations are on top, and ' + ' stations down the slope of the bank.

Station	Date	Depth (in.)	<i>Nemertinea</i>	<i>Nephtys cirrosa</i>	<i>Nerine cirratulus</i>	<i>Ophelia bicornis</i>	Other worms	<i>Eurydice pulchra</i>	<i>Bathyporeia sarsi</i>	<i>Haustorium arenarius</i>	<i>Urothoe grimaldii</i>	Dipterous larvae	<i>Mytilus edulis</i>	<i>Tellina tenuis</i>	<i>Hydrobia ulvae</i>
BH - 100	23. viii.	6	.	.	6	67	.	24	6	.	.	.	.	.	.
BH - 50	23. viii.	7	.	.	6	25	.	42	2	.	.	1	.	1	.
BH + 4	25. vii.	6	.	.	4	19	1	10	1	.	.	.	.	.	.
BH + 9	25. vii.	6	.	.	2	53	.	29	.	.	.	1	.	.	.
BH + 14	25. vii.	6	1	.	8	43	.	27	2	.	.	.	.	.	.
BH + 19	25. vii.	6	2	1	7	14	.	32	2	1	.	.	1 <i>j</i>	3	4
BH + 24	25. vii.	6	.	3	8	.	1	3	24	1	19	.	.	13	.

The fauna (Table VIII and Fig. 10) was very poor, this being perhaps due to:

(i) Strong currents, which prevent the establishment of an epifauna.
(ii) The coarse and loose texture of the soil. Watkin (1942) found that coarser grades of sand usually supported a poorer fauna than was found in finer grades.

(iii) Drainage. This would seem to be an important factor in restricting typically intertidal species to low-water mark.

On top of the bank typical species were (Station BH - 100):

	Per m. ²		Per m. ²
<i>Nerine cirratulus</i>	24	<i>Eurydice pulchra</i>	96
<i>Ophelia bicornis</i>	268	<i>Bathyporeia sarsi</i>	25

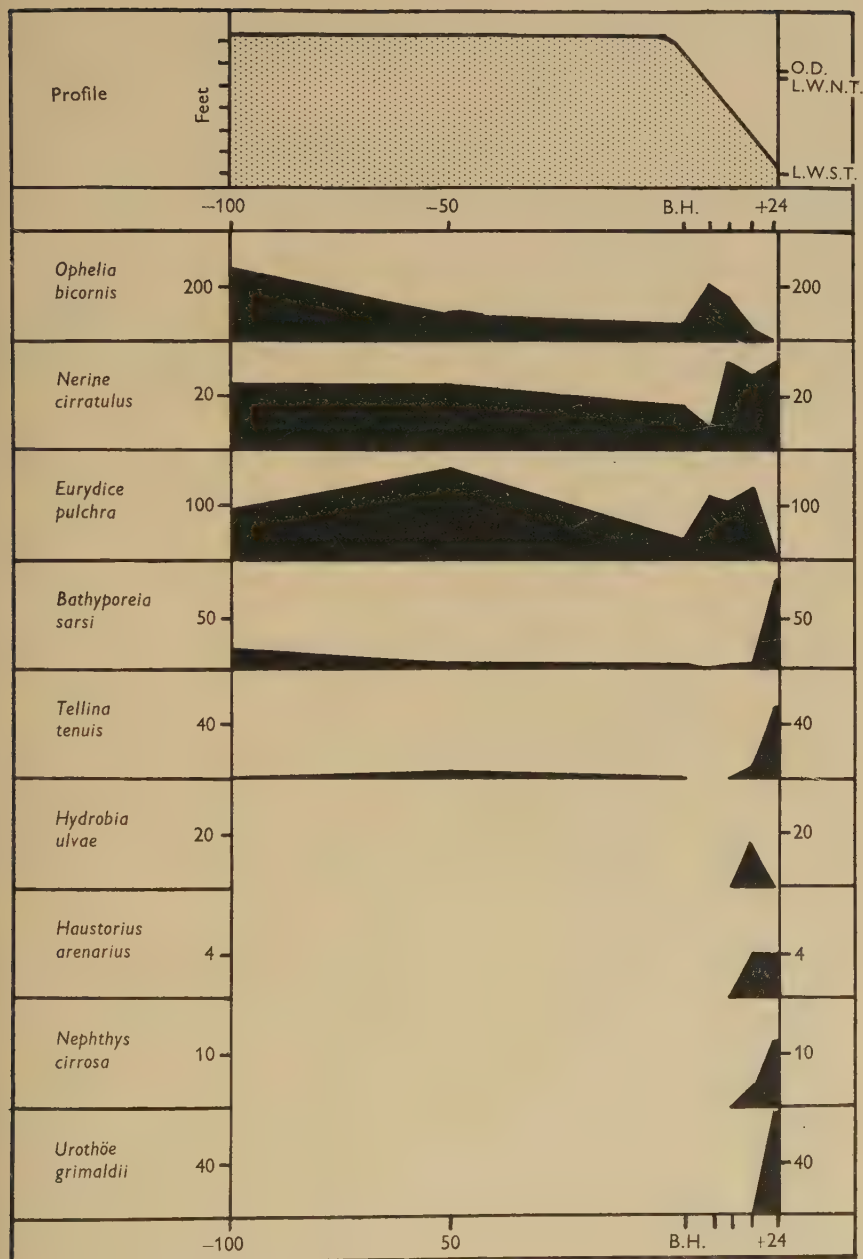


Fig. 10. Profile and fauna on Bull Hill Bank. Note that many typically intertidal species are here restricted to low-water mark. Numbers per m.²

At low-water mark *Ophelia* was absent, but certain other species appeared:

<i>Nephtys cirrosa</i>	<i>Tellina tenuis</i>
<i>Haustorius arenarius</i>	<i>Hydrobia ulvae</i>
<i>Urothoe grimaldii</i>	

The only abundant species on the bank was *Ophelia*, which occurred all over the top, buried to a depth of about 4 in. in the sand. It seemed to be most abundant in the valleys between the ridges in the sand.

Flora

Neither Bull Hill nor the area covered by the intertidal traverse had any significant growth of surface algae. The following species have kindly been identified by Dr M. Parke from material collected on the main traverse on 29 August 1947:

I-100. Algae absent.

I-78 → III. Minute dark green algae occurred, with a maximum abundance at about Station I. The algae increased in abundance during the summer and tended to bind the surface layer of sand. Species recorded:

Merismopedia glauca Kütz
Oscillatoria margaritifera Kütz

III + 15. Patches of *Enteromorpha crinita* J.Ag.

IV → IV + 33.

Oscillatoria margaritifera Kütz
Enteromorpha crinita J.Ag.
E. intestinalis Link.

IV + 75 → VI. *Zostera nana* Roth

Z. Hornemanniana Tutin

Drifting algae, or fragments of them, stranded by the receding tide, add to the organic content of the banks.

The following species were found deposited on the traverse:

<i>Enteromorpha crinita</i> J.Ag.	<i>Ceramium rubrum</i> Ag.
<i>E. intestinalis</i> Link.	<i>Callithamnion corymbosum</i> Lyngb.
<i>Ulva lactuca</i> Linn.	<i>Ectocarpus confervoides</i> Le Jol.
<i>Chaetomorpha litorea</i> Cooke	<i>Isthmoplea sphaerophoia</i> Kjellm.
<i>Lomentaria clavellosa</i> Gaill.	<i>Fucus vesiculosus</i> L.
<i>Gracilaria confervoides</i> Grev.	

Large areas of the mud-flats in this part of the estuary were covered by *Zostera*, which occurred mainly between high- and low-water mark of neap tides. No *Z. marina* L. has been found in the estuary.

Spartina stricta Roth. is native in the area north of the Warren, but *S. Townsendii* Groves has been planted. 1000 setts of the latter were planted out near the Warren in November 1935 to stabilize the mud-flats. *S. Townsendii* is spreading slowly along the edge of the Warren, and a careful examination revealed small clumps along the whole of the northern side of the Inner

Warren. In the traverse area, about 200 yards square, twenty-three plants or small clumps were found. These occurred on the sand or among the *Zostera*, mostly at about H.W.M.N.T.

BIOMASS AND SOURCES OF FOOD

The 'rough weight' of the principal species at certain stations was determined by weighing preserved specimens after removal of surface moisture. The shells of lamellibranchs were removed before weighing. The species comprising the 'epifauna' were not included. Details of biomasses are in Table XII.

On sand at Station I-100 the biomass was 4.6 g./m.², this being by far the poorest area. On Bull Hill Bank, however, where *Ophelia* was abundant, a total of 36.9 g./m.² was reached, this being almost entirely made up of these worms. At Stations II, IV and VI, the biomasses were 69.3, 101.7 and 45.4 g. respectively. The greatest weight at these stations was made up by only four species, *Arenicola*, *Scrobicularia*, *Cardium* and *Ampharete*. It would seem that 'soil-swallowers' such as *Ophelia* and *Arenicola* have a very efficient mode of feeding, as they outweigh all other species combined at their zone of maximum abundance. Carnivores (*Nephtys*, *Glycera*, *Eurydice*, etc.) are nowhere abundant, comprising about 5-10% of the total weight.

MacGinitie (1935), discussing food relations in a Californian estuary, found that carnivores comprised about 5% by weight of the total population of a mud-flat. Detritus-feeders made up the greatest weight of the population, probably on account of their longevity. MacGinitie considered that the main sources of food were *Zostera*, *Enteromorpha*, *Polysiphonia* and pieces of algae which floated in with the tide. Very few animals lived directly on these plants, the filter-feeders subsisting mainly on plants in various stages of decay, and on bacteria. *Zostera* appeared to be of use not only as a source of detritus, but also for its part in the accumulation of detritus which becomes caught around its roots. Hence it was in and near the *Zostera* regions that the greatest abundance and variety of life was found. At low tide plant tissue tended to become dried up and killed; dead leaves started decomposing into detritus, and meanwhile would be distributed by the action of animals and by water movements, so becoming available to all the bottom animals in the neighbourhood.

Although no attempt has been made to assess the relative roles of detritus, bacteria and plankton as the food supply of animals in the Exe Estuary, it is clear that conditions are not unlike those in the Californian estuary. The settling of drifting algae on the banks has already been referred to, and the importance of *Zostera* as a source of food for areas outside its habitat was emphasized by some observations made in August 1947. During the neap tides of that month some parts of the *Zostera* beds were left uncovered for several days during hot sunny weather. When again covered by the tide some of the leaves, which had become dry and black, became detached and floated

away. At this time leaves of *Zostera* were quite abundant floating up and down the estuary with the tide, being deposited on the banks as the tide receded.

NOTES ON CERTAIN SPECIES

The distribution of certain estuarine species is discussed by Spooner & Moore (1940), and of sand-living species by Watkin (1942). The following notes are intended to supplement these in the light of subsequent work and the results obtained in the present survey.

POLYCHAETA

Phyllodoce maculata (L.)

Fauvel (1923) regards *P. maculata* (L.) and *P. teres* Malmgren as one and the same species, although they were recorded separately by Allen & Todd (1902). In 1901, *P. teres* was found in clean sand above Starcross, in sand west of the mouth of Salthouse Lake, and from gravel between Powderham and Starcross. A specimen doubtfully assigned to *P. maculata* was taken on the sandy ground between Starcross and Cockwood.

The specimens found in 1947 were probably of the same species as those previously taken, but identification was difficult as many of the specimens were fragmented. *Phyllodoce* was found on the more muddy part of the main traverse, from Stations III+67 to VI+3. It was not found on Bull Hill.

Eteone longa (Fabricius)

In 1901 Allen & Todd found specimens identified as *E. pusilla* Örsted (*nec* Malmgren) in clean sand; and it seems likely that the 1947 specimens were of the same species as found in 1901, but there is some doubt as to their identity. Those found in 1947 had a head approaching that described by Malmgren (1865) for *E. pusilla*, but the anal cirri are not '*lineare-fusiformes elongati*', but of the type described by Örsted (1843) as '*papillis caudalibus subglobosis*'. The head does not correspond with Örsted's description, however. Fauvel (1923) does not refer to *E. pusilla* Örsted, and *E. pusilla* Malmgren is now *E. lactea* Claparède.

The specimens correspond most closely to *Eteone longa* (Fabricius), both in the shape of the head and of the anal cirri, and it is to this species that they have been provisionally assigned.

Eteone extended from sand to mud on the main traverse. Intertidally it ranged from about H.W.M.N.T. to about L.W.M.N.T., with a maximum near the upper part of its range. It was absent from Bull Hill.

Nephtys hombergi Lamarck

This species was recorded by Allen & Todd from sand and muddy sand all over the estuary, but not in very muddy ground.

In 1947 it was collected at stations ranging from sand to mud. Its maximum

density was at IV + 33: 104 per m.²; with a silt content of 9.4%. It was less abundant, c. 12 per m.², at IV, where the silt content was 16.6%, and was absent on muddy stations with *Zostera*, where the silt percentage ranged from 11.2 to 22.6. At the other end of the traverse it did not extend beyond I + 30, possibly being limited by the better drainage at this end. Intertidally it ranged throughout the tidal zone, with no distinct maximum. It was not found on Bull Hill.

This species is not confined to the shore, being common on sandy and muddy bottoms at sea. Spooner & Moore (1940) and Alexander, Southgate & Bassindale (1935) have found it plentiful towards the mouth of the estuaries of the Tamar and Tees respectively. On the Tamar its normal density was between 200 and 300 per m.², rather higher than that met with on the Exe. Brady (1943), however, found the maximum density of this species at Black Middens on the Northumberland coast to be only 60 per m.²

Nephtys cirrosa Ehlers

Found by Allen & Todd only in fine, clean sand, where it was quite plentiful.

In 1947 this species was found in wet sand at stations between II and III + 33, the silt content ranging from 1.35 to 6.9%. Intertidally, it occurred at most stations, with its greatest density, 32 per m.², near low-water mark. On Bull Hill it was restricted to two stations near low-water mark. The intertidal range of this species thus seems to be dependent on drainage conditions in the sand.

There are few other records of this species. In the Plymouth Marine Fauna (Marine Biological Assoc., 1931) it is recorded from sand between tide-marks on Drakes Island and the Yealm Estuary. Bassindale (1938) found single specimens in sand near the mouth of the Mersey Estuary. Rees (1939) found it on a number of traverses on sandy shores in North Donegal; the species extended up the beach to half-tide mark, maximum numbers occurring at low-water mark.

Scoloplos armiger (O. F. Müller)

In 1901 this species was found in sand or muddy sand within the estuary, but not on the Pole Sands. In the 1947 survey it was found on soils ranging from 0.7 to 16.6% silt, but was absent at the muddiest stations. Its highest density was in muddy sand at III + 33: 108 per m.², the silt content being 6.9%. It did not occur on the well-drained sand, and was absent from Bull Hill. Intertidally it showed a maximum just below H.W.M.N.T.

The distribution of *Scoloplos* on the main traverse resembles that of *Macoma* and *Nephtys hombergi*, being typical of species with an optimum density in muddy sand, and being intolerant of 'pure' mud. It is recorded from muddy sand in a number of areas, but not from clean, sandy beaches, and it is usually less abundant in mud. Spooner & Moore (1940) found it in moderate numbers,

up to 152 per m.², on St John's Lake, where it seemed to be restricted to the upper tidal levels in the *Zostera* zone.

Brady (1943) found *Scoloplos* at Budle Bay on the Northumberland coast. It was widely distributed in slightly muddy sand, its density seeming to be inversely related to that of *Macoma balthica*. The author considered that the two species were in competition for detritus as food, but that since *Macoma* also fed on suspended detrital and planktonic matter, it tended to become the dominant species. Thus *Scoloplos* could only become really abundant where *Macoma* was for some reason scarce.

The density of *Macoma* on the Salthouse Lake traverse was nowhere great, so that competition for food between the two species was probably not very intense. On the whole, *Macoma* and *Scoloplos* show similar distribution and densities, so failing to agree with Brady's observations.

Nerine foliosa (Audouin & Edwards)

This species was recorded as *N. comiocephala* Johnston by Allen & Todd, several specimens being obtained in sand west of the mouth of Salthouse Lake and in the hard clayey mud to the north of it.

In 1947 small numbers were found on clean sand at Stations I-40 and I-3A, also among gravel above H.W.M.N.T. at B-3. None was found on Bull Hill.

There are few records of this species: Percival (1929) records it from the River Tamar, in mud; in the Plymouth Marine Fauna it is also recorded from Wembury, Drakes Island, east side of the Sound, Kingsand Beach, and the River Yealm sand bank. Brady (1943) found it in Budle Bay, a few occurring at about low-water mark in firm clayey sand.

Nerine cirratulus (Della Chiaje)

In 1901 specimens were found on Bull Hill Bank and Cocklesand.

In 1947 it was found in small numbers on the main traverse chiefly in clean, fairly well-drained sand near Station I. It did not occur in company with *Ophelia* on this traverse. On Bull Hill, however, it was more abundant, occurring at all stations, and was therefore occurring with *Ophelia*.

The distribution of this species is discussed by Watkin (1942), who finds it to have a wide intertidal range, with maximum densities about half-tide mark. Pirrie, Bruce & Moore (1932) describe a similar zonation on the sandy beach at Port Erin. It is recorded from muddy sand at Salcombe by Allen & Todd (1900), and in the Mersey Estuary by Bassindale (1938).

Pygospio elegans Claparède

Allen & Todd record this species in clean hard sand inside the estuary, but not on the Pole Sands.

Pygospio was found at nearly all stations on the main traverse, the maximum

density being at about Station I+67. It was rare or absent in loose sand, and was not therefore found on Bull Hill. In small numbers it ranged on to the muddy stations of the traverse, its requirements seeming to be merely the presence of a firm substratum and of sufficient sand-grains with which to construct its tube.

In the sorting dish a number of the worms emerge from their tubes a day or two after collection, but many more probably remain within their tubes. A rough estimate of numbers was made by determining the dry weight of sandy tubes at certain stations. (Sometimes the tubes were sorted out from the general collections, at other times a special collection was made by carefully sieving the top 2-3 in. of soil from an area close to the original station.)

There are few records of this species in Britain: if present in small numbers it might easily be overlooked. It has been found in various grades of soil near the mouth of certain estuaries. Percival (1929) records it from the River Lynher near Ince Castle, Bassindale (1938) found it in the upper estuary of the Mersey, and Allen & Todd (1900) found it in muddy gravel under the Marine Hotel at Salcombe. Beanland (1940) records it from banks near the mouth of the Dovey Estuary, where it occurred on soils ranging from 0 to 30.3% of silt-plus-clay.

Ophelia bicornis Savigny

Allen & Todd found *Ophelia* to be abundant on the north-eastern side of Pole Sands and on Bull Hill. Single specimens were found at three other stations in the estuary.

In 1947 it was found in small numbers (12 per m.²) on clean well-drained sand at Stations I-100 and I-40. On Bull Hill it was abundant at all stations except at low-water mark where it was absent. Its distribution was rather patchy, but a varying number could be dug up anywhere on top of the bank. The maximum density was 268 per m.²

The occurrence of *Ophelia* is clearly related to the degree of drainage of the sand, but Wilson (1948) has shown that the grade of soil may also affect distribution. Experiments with larvae of *Ophelia* show that they 'metamorphose most readily in sand from their natural habitat and with hesitancy or not at all in sands from other sources'. It is shown that the size and shape of the sand grains, or perhaps of the interstices, determines the readiness with which metamorphosis occurs. Wilson has found that sand from the Salhouse Lake area is less effective in bringing about metamorphosis than the coarser sand from Bull Hill Bank. Although the Salhouse Lake sand used in the experiments was probably not from the region where *Ophelia* occurs, it appears to be of a similar grade to that in which small numbers of *Ophelia* were found.

Thus the relative numbers of *Ophelia* in the two localities is explicable in terms of the soil grade.

... If this be so, we have a reasonable explanation of the observed distribution of *Ophelia* in the Exe estuary, a heavy concentration in the metamorphosis-stimulating sand of the Bullhill Bank and the Polesands, with a much lower concentration in the less stimulating Salthouse Lake area. As the larvae in the later pelagic stages drift over the banks the majority of these coming into contact with the Bullhill sand will enter it and stay there, but of those washed over the Salthouse Lake only a small proportion will settle, the majority will leave the sand after testing it and, continuing pelagic life, may later on eventually reach the Bullhill Bank or the almost equally suitable Polesands nearer the open sea. This explanation is at least as reasonable as supposing that there is an even settlement over the whole area followed by greater destruction of the young worms in the unfavourable soils, and the results of these experiments support it [from Wilson, 1948].

Arenicola marina L.

Allen & Todd recorded this species as abundant on most of the banks of the estuary, being scarce on Pole Sands and on a mud-bank near the top of the estuary.

In 1947 *Arenicola* was found at nearly all stations in the Salthouse Lake area. It was absent from the well-drained area where *Ophelia* occurred, from gravel near high-water mark, and from the bed of Salthouse Lake (H + 15). None was found on Bull Hill.

A comparison of numbers found by digging and by counts of casts has already been described (p. 206). On the main traverse the maximum density was 52 adults per m.², at Station III + 33, where the silt content was 6.9%. *Arenicola* was found in soils with 0.05–22.6% silt.

Intertidally it ranged from the edge of the gravel, at about H.W.M.N.T. down to low-water mark. At F-3 (half-tide mark) a density of 60 per m.² was recorded, there being only 0.6% of silt. Serventy (1934), describing the fauna of Scolt Head Island, found that *Arenicola* was scarce in soft muds with *Zostera*, in hard compact mud, and in clean sand. It did, however, occasionally occur on the open beach with *Ensis* and *Spisula*. Spooner & Moore (1940) found *Arenicola* to be scarce on the Tamar Estuary, where the soil contains very little sand, being almost entirely silt. Wells (1945) noticed that it was most abundant on sand where drainage was poor: where a stretch of sand dried out soon after the tide had receded, only small specimens were found.

Newell (1948) has recently investigated the life history of *Arenicola*. Fertilized eggs appear to be carried up the beach on the incoming tide and become lodged among pebbles or sand, where larval development probably takes place. The maximum spawning intensity at Whitstable is at neap tides (in October) so that the eggs tend to be deposited at high-neap-tide mark rather than in unfavourable environments higher up the beach. The larvae metamorphose in the following spring.

Casual observations in the Salthouse Lake area indicated that large numbers of small *Arenicola* did occur high up the beach (many well above high water of neap tides, however), suggesting that conditions are similar to those at

Whitstable. On the traverses numbers of small specimens occurred among *Zostera*, below the pebble zone at C+15, and on clean sand near Station I. Perhaps the pebble zone and the *Zostera* beds are 'nursery areas' where the larvae develop, subsequently migrating to the regions where the adults occur.

Ampharete grubei Malmgren

This species was not recorded by Allen & Todd. In Salthouse Lake it was abundant in the more muddy stations of the main traverse, reaching a maximum density of about 9200 per m.² at V-3, where the silt content was the highest in the traverse (22.6%). Its distribution was patchy, as only 4000 per m.² were found at the adjacent Station, V+3. *Ampharete* was abundant over a range of soils with silt concentrations of 6.9-22.6%. It was absent from Bull Hill.

There are few other records of this species: Serventy (1934) found a large colony in very soft mud at Scolt Head Island, while Spooner & Moore (1940) record up to 4000 per m.² at St John's Lake, from about mid-tide downwards. It did not penetrate far up the Tamar Estuary. Perhaps the scarcity of records of *Ampharete* is due to the few intertidal mud banks which are exposed to marine conditions; the species evidently having little tolerance of reduced salinity. The mud-flats at Salcombe would seem to provide a suitable habitat for this species, but none were found there by Allen & Todd (1900), although it is possible that *Ampharete* was overlooked among collections of *Melinna*.

Melinna palmata Grube

Allen & Todd found this species (recorded as *M. adriatica* von Marenzeller) in small numbers in the lower part of the estuary. In 1947 a few specimens were found on the more muddy parts of the Salthouse Lake traverse.

Like *Ampharete*, *Melinna* is absent from many muddy localities, but occurs in the Tamar and at Salcombe. Spooner & Moore (1940) found it together with *Ampharete* in the Tamar, but penetrating farther up-river than the latter; it was most abundant at low water at the edge of West Muds, where the density was 189 per m.²

CRUSTACEA

Eurydice pulchra Leach

This species seems to have been overlooked by Allen & Todd, perhaps on account of its small size.

In 1947 it was found on the main traverse in clean sand just below L.W.M.N.T., with a maximum density of 612 per m.² It was rare on the intertidal traverse. On Bull Hill it was quite plentiful, occurring at all stations, with a maximum density of 168 per m.² On this bank it thus ranges from half-tide down to nearly L.W.M.S.T.

This species has been recorded from clean sand above half-tide mark by Brady (1943), Watkin (1942), Rees (1939), Pirrie *et al.* (1932) and by Elmhirst (1931). Crawford (1937*b*), however, records it from sand about half-tide

mark downwards. Its intertidal distribution is perhaps related to the degree of drainage of the sand.

Elmhirst (1931) has shown that it has a pelagic phase; in winter it seeks shelter in the shallow water beyond low-water springs, and in summer it may swim in large numbers, following the flotsam at the edge of the tide. Watkin (1941*b*), however, states that they 'rise out of the sand with the inflowing tide, proceed to feed immediately and sink again into the sand with the retreating tide'.

Bathyporeia pilosa Lindström

The systematics of the genus *Bathyporeia* were somewhat confused before the publication of a paper by Watkin (1938), and records before 1938 are consequently unreliable.

Allen & Todd recorded *B. pelagica* Sp. Bate from collections with a mosquito-net trawl in the estuary, but the few available specimens are of *B. sarsi* (see notes under the latter species).

On the Salhouse Lake traverse *B. pilosa* occurred from Stations I-100 to II on clean sand. It was most abundant on the loose well-drained sand just below H.W.M.N.T., which was not covered by extreme neap tides. The maximum density was 2180 per m.² This species was absent from Bull Hill.

Beanland (1940) found it at several stations on the Dovey, the soil having a silt content of under 1%. The maximum density was 298 per sq.ft. At Kames Bay Watkin (1942) records a density of *c.* 17,000 per m.²

Species of this genus have a pelagic phase. Watkin (1939) found that in Kames Bay *B. pilosa* occupied a definite belt across the shore at a level above H.W.M.N.T. Tow-nettings made at high tide showed that the different species became pelagic, but each more or less retained its zonation, returning to its own area at low tide. Watkin (1938) gives a list of localities for this species.

Bathyporeia sarsi Watkin

This species is distinguished from *B. pilosa* by several minor characters, the most conspicuous being the shape of the basal joint of the antennule (which is relatively broader in *B. sarsi*) and by the number of groups of spines on the third epimeral plate. Specimens in the museum of the Plymouth Laboratory show that some of the specimens recorded by Allen & Todd (1902) as *B. pelagica* Sp. Bate were in fact what is now *B. sarsi* Watkin. The specimens in question were caught on 8 July 1901 between Cockwood and Bull Hill Bank.

On the Salhouse Lake traverse it occurred in moist sand from Station I+67 to Station III+33, thus slightly overlapping the *B. pilosa* zone. Intertidally it extended from about high-neap-tide mark downwards. The maximum density was at F-3 (half-tide mark) where there were 352 per m.² On Bull Hill it occurred at all but one station, the greatest density, 96 per m.², being at low-water mark.

A short list of localities is given by Watkin (1938); it is an intertidal or shallow water form.

Haustorius arenarius (Slabber)

Haustorius was found by Allen & Todd in Pole Sands, Shaggles Sand, and a sand north of the Warren.

In 1947 only five specimens were found; three in wet sand below half tide in the intertidal traverse, and two on Bull Hill near low-water mark.

This seems to be nowhere an abundant species; Watkin (1942) records 1 per sq.ft. near high-neap-tide mark in Kames Bay. Its intertidal distribution, which is variable, is discussed by Watkin.

Corophium arenarium Crawford

This species was created by Crawford (1937*a*) to distinguish a form closely resembling *C. volutator* (Pallas), but which occurs in sandy habitats. It is possible, and indeed likely, that *C. arenarium* was found in the 1901 survey but was included with *C. grossipes* L. (= *volutator*). *C. volutator* also occurs in this area (Crawford, 1937*c*).

On the Salthouse Lake traverses *C. arenarium* was found on a wide range of substrata, being scarce, however, on loose sand and on mud with *Zostera*. Its maximum abundance was at II + 67: 360 per m.², where the silt content of the soil was 2.2%. Intertidally it ranged from above H.W.M.N.T. to about half-tide mark. It was absent from Bull Hill.

Crawford (1937*a*) found it in firm but slightly muddy sand from half tide to L.W.M.N.T. It is recorded from the Dovey Estuary by Beanland (1940) and by Watkin (1941*a*). Watkin states that 'away from the influence of the streams and above the high-water mark of neap tides *Corophium volutator* is replaced by *C. arenarium*, which is the dominant species in the estuary. The two species may overlap at their limits of distribution; but at their centres of density, which in all cases are well marked, they remain unmixed'.

The occurrence of the two species in the same area seems to confirm the validity of *C. arenarium* as a separate species. Furthermore, Mr Spooner informs me he has observed additional morphological differences between them.

MOLLUSCA

Tellina tenuis da Costa

In 1901 *Tellina* was common on the west side of Pole Sands at low-water mark, and between Cocklesand and Lympstone mussel beds; a few were taken on Bull Hill, the Warren and Shaggles Sand.

In 1947 this species was found in moderate numbers on moist clean sand. The maximum density on the main traverse being 88 per m.² at II + 3. Intertidally it occurred up to nearly H.W.M.N.T., and extended down to low-water mark. Population densities in the lower half of the tidal zone were remarkably constant, averaging 184 per m.² On Bull Hill the species is restricted to a zone

near low-tide mark, but one individual was found on top of the bank. The length of shell of each specimen was measured to the nearest mm. 'above', the results being shown in Table XIII.

Tellina has been studied by Stephen (1928, 1929*a, b*, 1931). Populations in Kames Bay reached 1897 per $\frac{1}{4}$ m.², but elsewhere lower densities, averaging 250 per $\frac{1}{4}$ m.², are recorded by Stephen. In Kames Bay densities decreased from low- to high-water mark; large individuals occurring mainly at the higher levels, whereas many small animals were found at low-water mark.

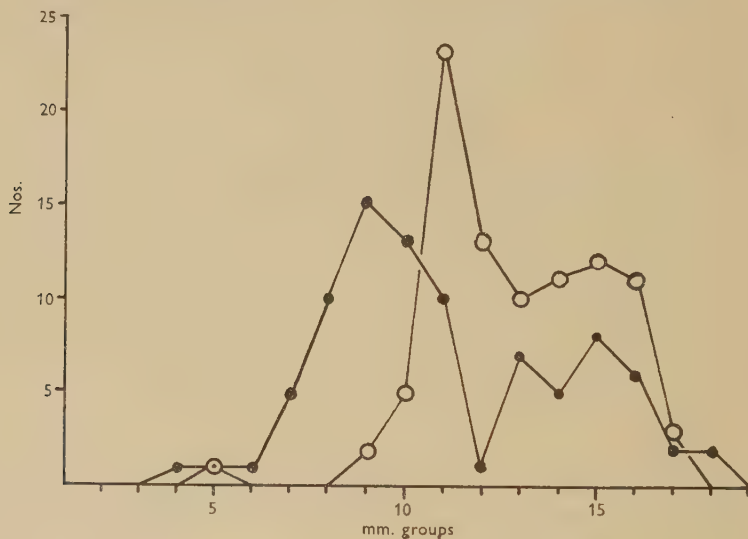


Fig. 11. Length-frequency distribution graphs for *Tellina tenuis* at Stations F (half-tide mark) and H (low-tide mark); 14 and 15 August 1947. Based on ninety-one individuals from F and eighty-seven from H. —○—, Station F; —●—, Station H.

The density of *Tellina* on Salthouse Lake was very much less than in areas studied by Stephen, numbers not being large enough to give statistically significant results after size-grouping. Comparison with Stephen's results, however, shows the following features:

(i) Population density decreased at higher levels on the beach; but up to about half-tide mark densities were uniform.

(ii) Measurements of shell length show that on the whole a greater proportion of the smaller size-groups occurred near low water. This is shown in Fig. 11. The maxima for what may be a year group occur at 9 mm. length at low-tide mark, but at 11 mm. length for individuals from half-tide mark, suggesting a greater growth rate in the latter position.

(iii) Stations at the same level on the main traverse showed little difference in the numerical proportions of the different size-groups, although the population density was variable.

The species has been found on a number of sandy estuaries and shores where there is some shelter from wave action. Rees (1939) found that the extent of its range up the beach from low-water mark was variable. This is probably related to drainage, as *Tellina* is restricted to low-water mark on Bull Hill where the drainage is very thorough.

Macoma balthica (L.)

In 1901 this was recorded (as *Tellina balthica* L.) from the mud flats between Rocklesand and Exmouth railway station, on mud, south of Lympstone mussel-bed, and on the west side of the estuary.

In the Salthouse Lake area it occurred on the main traverse on soils ranging from moist sand to mud. The maximum density was 24 per m.² at V-3, where the silt content was 16.6%. On the intertidal traverse it was restricted to a zone at about half-tide mark, but two were found in the bed of Salthouse Lake. It was absent from Bull Hill.

Comparable densities, up to 36 per m.², were recorded by Spooner & Moore (1940) from St John's Lake, where it was fairly evenly distributed through the tidal zone. As on the Exe, few spat were found. Population figures for other areas, quoted by Spooner & Moore, show that very much higher densities may occur. Beanland (1940) found populations up to 657 per sq.ft. in the Dovey, over a soil range from 0-32.4% silt, with maximum densities where there was 2.5-4.3% silt. Brady (1943) showed an inverse relation between densities of *Macoma* and of *Scoloplos*, which is discussed in the notes on the latter species.

Macrobicularia plana (da Costa)

This was recorded by Allen & Todd (as *S. piperata* (L.)) as one of the commonest bivalves of the estuary.

On the main traverse it occurred at all stations from III to VI, on mud and lummy sand; and small individuals (under 10 mm. long) also occurred on wet sand from I to III. It reached its maximum abundance at IV+33, where there were 156 'adults' and 72 'young' per m.² Intertidally it occurred over a fairly narrow range at about half tide, and was absent from Bull Hill. Measurements of shell-length are shown in Table XIV.

Spooner & Moore (1940) state that this species is characteristic of estuaries in the south and east of England, but is scarce and more local in the north. In the Tamar conditions for settlement of spat seemed to be most favourable at the seaward end of the estuary, while growth conditions were at an optimum much higher up the estuary. The great majority of spat settling on St John's Lake, near the mouth of the estuary, die off at an early age.

Cardium edule L.

Cockles are plentiful in the estuary: Allen & Todd recorded them in profusion from Cocklesand, Bull Hill Bank, and along the west side of the estuary.

In the Salthouse Lake area *Cardium* occurred on a wide range of soils, from clean sand to mud, and from high-water mark of neap tides down to the bed of Salthouse Lake. It was absent from well-drained sand at one end of the main traverse, and from Bull Hill Bank (the cockle bed is farther to the north, on the gravelly part of this bank).

Its maximum abundance was in mud at Station VI-3, where there were 136 small and 60 adults per m.² The length of the shells of individuals at each station is given in Table XVI.

A limited amount of cockle gathering occurs in the Salthouse Lake area.

Hydrobia ulvae (Pennant)

In 1901 this was recorded from nearly all grounds in the estuary.

Its distribution on the main traverse is clearly related to the presence of *Zostera*, which provides shelter and may be a source of food. Its maximum abundance was 16,000 per m.². Outside the *Zostera* beds it was much less abundant, and it was absent from areas scoured by currents, such as the bed of Salthouse Lake and the top of Bull Hill. Intertidally, it was mainly concentrated towards H.W.M.N.T. *Hydrobia* has the habit of floating upside down from the surface film, and may in this way be dispersed away from the *Zostera* beds to the sandy areas, which are not its normal habitat.

The distribution of this common estuarine species is discussed at length by Spooner & Moore (1940).

DISCUSSION

A study of the fauna of the main traverse on Salthouse Lake has shown that the distribution of burrowing species is closely linked with the nature of the soil. Drainage may be of importance at one end of the traverse, but most of the stations had standing water on the surface at low tide.

Although conclusions as to the role of the soil as a limiting factor can only be applied with confidence to the area investigated, they should also apply (modified by divergencies in other factors) to the fauna of other areas. The great value of the Salthouse Lake traverse lay in the opportunity it offered for a study of the influence of soil grade on distribution, the effect of other factors being eliminated owing to the peculiar local conditions.

A striking example of the influence of silt on distribution is exhibited by the difference in the fauna on either side of Station III. On one side was an area with a silt content of under 2.5%, and on the other side there was over 6.5% silt. This difference is clearly shown in the distribution of certain species. Thus *Bathyporeia sarsi*, *Urothoe grimaldii* and *Tellina tenuis* were restricted to the former area, whereas *Ampharete grubei* and *Melinna palmata*

occurred only in the latter area. Some species, more tolerant of variable silt concentrations, ranged across the two areas, but these often showed a marked change in density.

The apparent correlation between distribution of animals and silt content, however, can establish neither the degree to which silt can be regarded as a limiting factor, nor its method of operation. The observed distribution of species may be related to: (i) a direct effect of silt on distribution; (ii) an indirect effect of silt, through its effects on the type of vegetation, consistency of the soil, drainage, or some chemical or physical factor in the soil; (iii) some other factor of which silt may merely be an indicator. With regard to the last, the organic content of a soil is probably closely related to the quantity of silt, since both fine organic matter and silt tend to settle in the more sheltered parts of an estuary. In grade analysis much of this organic matter will be represented in the silt fraction, though it would appear that in the samples dealt with here much of the silt was of inorganic origin.

It would seem possible that silt as such limits the inhabitants of clean sand to their normal habitat, whereas the mud-living species are restricted to the muddy areas on account of the abundant food supply in the form of detritus.

As yet very little is known of the action of the factors limiting the distribution of intertidal animals, but they presumably operate in one of three ways: by their influence on the settling reactions of planktonic larvae, by their effect on the migration of adults, or by affecting mortality after metamorphosis. *Ophelia* has already been cited as an example of a species whose distribution and density is partly determined by the settling reactions of the larvae. Lamellibranchs probably move about to a considerable extent after metamorphosis, and their distribution may be related to a choice of the more favourable grounds during the course of their wanderings.

Chapman & Newell (1947) have emphasized the possible importance of the 'thixotropic' properties of a soil in relation to the burrowing of *Arenicola*. The ease with which a burrower can penetrate the soil is enhanced by the capacity of thixotropic soils to decrease their resistance to penetration immediately after agitation. The thixotropic properties of a soil depend upon a high water content and also upon the presence of small quantities of colloidal substances. At Whitstable, as on Salthouse Lake, a layer of clay occurs beneath the surface, and this is believed to supply these colloidal substances to the soil. Thus the presence of small quantities of silt or clay may profoundly alter the properties of a sand and hence its suitability for burrowing species.

At one end of the main traverse there is a marked change in the fauna of the clean sand, which is almost certainly due to the better drainage conditions in this area. Most of the species common on the rest of the traverse are absent, but *Ophelia* occurs here and nowhere else on Salthouse Lake. Thus the distribution of *Ophelia* and intertidal species such as *Tellina* would appear

to be complementary, the one depending on a well-drained, the other on a water-saturated soil. This is emphasized by the distribution of these species in the extremely well-drained sand on Bull Hill Bank. Here *Ophelia* extends almost to low-water mark, but wherever the soil is wet, *Ophelia* is absent and *Tellina* appears.

The intertidal distribution of many species cannot, however, be explained in terms of drainage conditions. Thus *Bathyporeia pilosa* occurs only in a zone at high-neap-tide mark, although *Eurydice*, which exhibits a similar zonation on Salthouse Lake, ranges down to low-water mark on Bull Hill.

SUMMARY

Erosion of Dawlish Warren, at the mouth of the Exe Estuary has resulted in a redistribution of sand, which has come to lie in close proximity to certain of the original mud banks.

Quantitative collections of the macrofauna were made along a traverse passing from the newly deposited sand to the old mud bank, stations all being at about half-tide level.

Measurements of salinity, temperature, pH, currents and wave action show that these are similar for all stations. Thus it has been possible to observe the distribution of the fauna in relation to the type of soil without the usual complications due to differences in other factors.

The occurrence and density of many species is shown to be correlated with the silt content of the soil, or some factor related to it. A traverse extending from high- to low-tide marks was worked in the same area. This provides information on the intertidal distribution of species occurring in the main traverse.

An additional traverse was worked on Bull Hill Bank, a sand bank which is much scoured by currents. The distribution of the fauna on this bank emphasizes the importance of soil drainage on distribution.

The distribution of certain species is discussed in the light of data obtained from other areas. No marked changes in the fauna of the estuary seem to have occurred since a survey of the estuary was made by Allen & Todd in 1901.

The possible mode of action of limiting factors is briefly discussed.

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EXPLANATION OF PLATES

PLATE I

(By kind permission of the Under Secretary of State for Air)

Aerial photograph of the lower part of the Exe Estuary, taken at low tide, 3 August 1945. Submerged parts of some of the sand-banks are visible under water. Langstone Point: bottom left; Exmouth: centre right. Bull Hill is slightly to the left of the centre, and Dawlish Warren is below it. The remains of Warren Point are seen separated by a narrow channel from the rest of the spit.

PLATE II

(By kind permission of the Under Secretary of State for Air)

Aerial photograph of Dawlish Warren, 13 April 1946. Warren Point has been almost completely washed away. Note the sand distributed in a north-westerly direction from the breach. Photograph taken with water at about high-neap-tide mark. Bull Hill Bank is seen top-centre; note the ridges on its surface.



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APPENDIX

TABLE IX. SURFACE SALINITIES (PER MILLE) IN THE EXE ESTUARY
(SEE ALSO FIG. 1)

The stations 'A' to 'I' are those indicated on the top of Fig. 1. The column marked 'position' gives the distance of each station from Exmouth Pier, in miles. The readings taken in 1947 were taken during a period of drought when the River Exe was very low: those taken in the spring of 1948 when the river was at about normal level. The time each reading was taken, relative to the time of high or low tide, is indicated in italics under the salinity readings. Thus -15 is 15 min. before, and +45 is 45 min. after high or low water. The time and height of high tide are also given. (The readings made on 5 July 1947 are not given in Fig. 1.)

Date	...	5. vii. 47	18. vii. 47	27. vii. 47	28. viii. 47	3. ix. 47	3. iii. 48
Time of high tide	...	7.47 a.m.	6.31 a.m.	1.42 p.m.	4.23 p.m.	8.03 a.m.	11.30 a.m.
Height	...	11 ft. 2 in.	12 ft. 2 in.	9 ft. 6 in.	10 ft. 2 in.	12 ft. 5 in.	10 ft. 2 in.
State of tide	...	Low	Low	High	Low	High	High
Station	Position (miles)						
A	0	27 -15	32 -50	34 -52	—	34.5 -23	35 -15
B	0.35	27 -10	30 -45	34 -13	32 -25	34.5 -18	35 -8
C	1.0	24.5 0	28 -30	34.5 -23	30.5 -15	34.5 -3	34 +1
D	1.7	24.5 +10	27 -17	34 -17	29 -5	34.5 +2	31 +8
E	2.5	20 +20	23 -6	31 -9	27 +3	34.5 +12	24 +18
F	3.0	20 +30	20.5 +2	31 -3	24 +9	34 +17	22 +24
G	3.7	16 +45	13 +30	30 +8	18.5 +25	32.5 +30	16 +37
H	4.85	12 +60	8 +48	22 +22	12.5 +34	32.5 +42	1.5 +51
I	6.5	1.5 +75	1.5 +68	11.5 +39	6.5 +50	25 +57	0 +75

TABLE X. COMPARISON OF SOIL ANALYSES AS MADE HERE WITH
RESULTS OBTAINED, USING A 70 I.M.M. SIEVE (0.2 MM. MESH)

Samples from Station II. Percentages by weight.

Grade (mm.)	Percentage	Grade (mm.)	Percentage
Over 2	—	Over 2	—
2-0.5	1.1	2-0.5	1.1
0.5-0.256	13.9	0.5-0.2	53.6
0.256-0.22	21.2	—	—
0.22-0.02	62.2	0.2-0.02	44.2
<0.02	1.6	<0.02	1.2

TABLE XI. TEMPERATURE AND SALINITY READINGS AT STATION III,
19 AUGUST 1947 (SEE ALSO FIGS. 4 AND 5)

C., station covered—sample from overlying water; U., station uncovered—sample from small pool.

Time	State	°C.	Salinity	Time	State	°C.	Salinity
7.40 a.m.	C.	19	34.5	2.20 p.m.	U.	27.25	36
8.05	C.	19	35.0	3.30	U.	27.25	37
9.05	C.	19	35.5	4.25	U.	26	38
10.10	C.	19.5	34.5	5.25	U.	24	36.5
11.10	C.	21	34.5	6.10	C.	21	35
12.45 p.m.	U.	25.5	36.5	6.55	C.	20.5	36
1.10	U.	26.5	36.5				

TABLE XII. TEMPERATURE AND SALINITY IN THE MAIN CHANNEL,
NEAR BULL HILL BANK, 19 AUGUST 1947 (SEE ALSO FIGS. 4 AND 5)

Time	°C.	Salinity	Time	°C.	Salinity
7.30 a.m.	18.75	35	2.30 p.m.	22.5	32.5
8.00	18.75	35	3.45	21.5	32.5
9.00	19	34.5	4.35	21	33
10.05	18.75	34.5	5.35	20.5	34.5
11.00	19	34.5	6.35	20	34.5
12.35 p.m.	19.75	34.5	7.00	20	34.5
1.35	20.5	34			

TABLE XVI. CARDIUM EDULE. NUMBER OF INDIVIDUALS IN EACH MM. LENGTH GROUP

FAUNA OF THE EXE ESTUARY

237

Length (mm.)	I-100	I-40	I-3B	I-3A	I+3	I+8	I+30	I+67	II-3	II+3	II+33	II+67	III-3	III+3	III+33	III+67	III-3	III+3	III+33	III+67	IV-3	IV+3	IV+33	IV+80	V-3	V+3	VI-3	VI+3	A-3	B-3	C-3	C+3	C+15	D-3	D+3	E-3	E+3	F-3	F+3	G-3	G+3	H-3	H+3	I-35							
2	.	.	.	2	2	2	4	2	I	.	I	5	.	3	3	15	.	.	.	.	.	.	.	37	.	.	2	2	23	.	.	.	.	.	.	10	13	2	2	.	.	.	.	.	.	.	.	.			
3	.	2	3	5	2	2	2	2	.	.	.	.	.	I	3	15	2	.	.	.	.	.	.	.	.	8	5	2	2	23	.	.	.	3	.	.	10	13	2	2	.	.	.	.	.	.	.	.			
4	.	.	I	6	2	2	3	2	.	.	.	.	.	.	3	15	6	.	.	.	.	.	.	.	.	21	5	3	2	23	.	.	.	5	45	.	.	.	.	.	.	.	.	.	.	.	.	.			
5	.	.	.	3	2	.	.	I	.	I	I	.	.	I	3	15	6	.	.	.	.	.	.	.	16	5	7	4	7	2	.	.	.	2	45	.	.	.	.	.	.	.	.	.	.	.	.	.			
6	.	.	.	.	I	.	.	.	.	I	I	.	.	I	3	15	.	.	.	.	.	.	.	.	9	11	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.			
7	.	.	.	I	.	I	.	.	.	.	I	.	.	.	I	15	.	.	.	.	.	.	.	.	10	3	4	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.			
8	.	.	.	.	.	2	I	.	I	.	.	.	.	.	.	15	.	.	.	.	.	.	.	.	10	3	4	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.			
9	.	.	.	.	.	.	I	.	I	.	I	.	.	.	.	9	.	.	.	.	.	.	.	.	I	10	4	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	I	10	4	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	I	11	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	.	.	.	.	.	.	.	.	I	12	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	.	.	.	.	.	.	.	.	I	13	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	14	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	15	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	16	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	17	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	18	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	19	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	20	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	21	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	22	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
23	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	23	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	24	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	25	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	26	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	27	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	28	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	29	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	30	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
31-35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	I	31-35	2	2	2	.	.	.	I	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Figures in italics unreliable owing to subsampling error.

A PRELIMINARY REPORT ON THE PLYMOUTH MARINE AND BRACKISH-WATER ROTIFERA

By E. D. Hollowday, F.R.M.S.

(Text-figs. 1-2)

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INTRODUCTION

Throughout the sixty odd years during which the Plymouth Laboratory has been the centre of the scientific investigation of British marine life, especially that of Plymouth Sound and neighbouring areas, there has only been one species of rotifer recorded,¹ namely *Synchaeta gyrina* Hood (Marine Biological Association, 1931, p. 149), but some doubt is cast on the accuracy of this identification by the mention of it occurring 'with eggs'. It is a well-established fact that *S. gyrina* does not carry its eggs after extrusion, but drops them immediately, although several closely related species are known to carry the eggs attached to the cloaca until they hatch. On the other hand, 'with eggs' may possibly mean that specimens were observed with the egg developing within the ovisac, in which event there is no objection to the identification. Anyhow, it is highly probable that *S. gyrina* actually occurs either in the Sound or the Hamoaze, although it was not observed during the writer's survey.

The dearth of information on the Plymouth brackish and marine Rotifera is probably not so surprising as it may at first appear, as none of the pelagic

Shortly after completing this report, two unpublished records by the late David Bryce were forwarded to the writer from the Plymouth Laboratory. These relate to the occurrence of *Synchaeta vorax* and *S. triophthalma* in the Sound during April 1934, and there is a doubtful record of *S. cecilia* Rousselet occurring beyond the Plymouth breakwater in March of the same year. Although this species was not refound by the writer, it is common in the Liverpool area (per A. L. Galliford) and it is highly probable that it does occur at Plymouth.

species found by the writer (with the possible exception of *S. vorax* Rousselet) ever become really numerous in the plankton, and, furthermore, there have been no serious students of the rotifers round our coasts since the death of Charles Rousselet, and very few before him. It is quite likely that workers at the laboratory specializing in plankton studies occasionally come upon rotifers in tow-net samples, but, being occupied with other forms, pay little attention to them. If this is so, the writer would gladly welcome rough sketches of any species noticed by workers on other phyla during their studies.

The writer wishes to emphasize that, although a considerable number of fine plankton samples have been examined at all times of the year, not to mention scrapings of algae from rocks and rock pools, at Jenny Cliff, Rum Bay, Barn Pool, and various locations in the Hamoaze, etc., the investigations carried out have only been of a preliminary nature. The Yealm, Cattewater, and upper reaches of the Tamar have not been looked into at all, and the apparent poverty of the brackish rotatorian fauna at Plymouth may be due to insufficient investigation.

The writer wishes to place on record his very deep gratitude to those who have been of great assistance in the compilation of this preliminary survey; to Mr F. S. Russell, F.R.S., for his kindness in allowing the writer unrestricted facilities at the Plymouth Laboratory; to Dr M. V. Lebour for a tube of preserved *Synchaeta* from Plymouth Sound plankton samples; to Mr S. M. Nunn for setting aside plankton samples from the laboratory's boats as required; and to Mr A. L. Galliford of Liverpool to whom the writer is indebted for general information on many aspects of the study of rotifers, for placing at his disposal information concerning the coastal Rotifera of the Liverpool area, for advice, and also for checking and criticizing the present report.

HISTORICAL SURVEY

Our knowledge of marine and brackish-water Rotifera dates back to the first half of the nineteenth century. In 1830, a certain Dr Michaelis collected a species of *Synchaeta* (which has more marine and brackish representatives than any other known genus of rotifers) in Kiel harbour. This discovery, and its subsequent publication as *Synchaeta baltica* by C. von Ehrenberg (1834, p. 220), led to a great deal of confusion regarding the identity of several other species of *Synchaeta* found in coastal waters during the next sixty years, and the matter was not really cleared up until Charles Rousselet (1902) published his monograph on the genus. The writer has not had access to the original description of *S. baltica*. In his *Die Infusionsthierchen* of 1838 (p. 439; Pl. 53, fig. 5), Ehrenberg is mainly concerned with the rotifer's supposed luminosity, originally suggested by Michaelis, but finds little support for the theory. The luminosity was doubtless due to the presence in the same water of

phosphorescent dinoflagellates, which, Ehrenberg states, were collected with the rotifers. Even so, P. H. Gosse (1856, p. 274, pl. xiv), and several other workers, apparently clung to the idea of *Synchaeta* spp. being responsible for luminous phenomena in coastal waters. Rousselet (1902) states, however, that there is no valid reason for the statement that this *Synchaeta*, or any other rotifer, is connected with the luminosity of the sea'.

During the period 1838-60, little work appears to have been done, apart from the occasional papers of P. H. Gosse and Dujardin, but in 1886, Hudson and Gosse published their monograph *The Rotifera or Wheel Animalcules*, and the supplement issued in 1889 contains drawings and descriptions of several species which Gosse had found in tidal pools along the Devon coast. Some of these are also known from fresh-water habitats. The publication of *The Rotifera* stimulated a great interest on the part of amateurs and professionals alike during the closing years of the nineteenth century. On the continent Dr Karl Zelinka, Dr Plate, and Zacharias, not to mention K. M. Levander and Robert Lauterborn, considerably advanced rotatorian anatomy, physiology, ecology and taxonomy; while John Hood, Charles Rousselet, and David Bryce extended our knowledge of the British fauna. Nearly all the above-mentioned workers described coastal forms, and in the report of the German plankton expedition of 1895 (Zelinka, 1907) is published a description and figure of a new species of *Synchaeta*, namely *S. atlantica*, which was collected at several stations in mid-Atlantic.

The years 1859, 1868, and 1876 are important milestones in the study of coastal Rotifera. In 1859, A. E. Grube published a description of a peculiar rotifer, *Seison nebaliae*, found as an ecto-parasite (probably only commensal) on the malacostracous crustacean *Nebalia*. In 1876, Claus described another species of this genus. In 1868, E. Ray Lankester described a rotifer, now known as *Zelinkiella* (*Discopus*) *synaptae*, from the alimentary canal of a sea cucumber. These two genera, along with the genus *Paraseison*, are the only exclusively marine rotatorian genera. The above-mentioned rotifers are highly specialized, and it is likely that careful examination of macroscopic marine animals may reveal further parasitic and commensal rotifers.

The published work on the Rotifera since the first years of the present century has been mainly devoted to the physiology, ecology and systematics of fresh-water forms, the only marine studies being those of Remane (1929) at Kiel, Vulfert (1942) in Germany and Italy, and Galliford (1945, 1946) in Liverpool Bay and along the Cheshire coast. A preliminary survey of rotifers from tidal pools at Millport was made by the late David Bryce in 1927 (Scottish Marine Biological Association, 1928).

COLLECTING AND OTHER METHODS

As with most other forms of life, the methods and apparatus used in collecting rotifers have to be varied according to the habitat. The pelagic species were collected by fine bolting-silk tow-nets, either from the laboratory's boat or by the writer from a rowing boat. The former collections were made at various stations in Plymouth Sound, from inshore to beyond the breakwater. The writer's own plankton hauls were made in the mouth of the Tamar, at various points in the Hamoaze, and from Drake's Island to the shore. Scrapings of algae from tidal pools and crevices along the shore at Barn Pool, Cremyl, Rum Bay, Jennycliff Bay, and the Royal William Victualling Yard wharfs, were taken and examined for the weed-haunting littoral forms. Masses of *Fucus* from all the above-mentioned stations were washed and squeezed through bolting silk in order to dislodge browsing forms. Collections were also made with a hand-net of fine bolting silk in the creek known as Stonehouse Lake.

Samples were always examined in fresh condition. It is a great mistake to preserve plankton samples when searching for Rotifera if there is any means of examining them within a reasonable time. This applies not only to marine, but to brackish and fresh-water samples also. Indeed, it is highly probable that many rotifers are overlooked by workers who would otherwise notice them, as a result of specimens being contracted or otherwise distorted through preservation. Furthermore, and this applies especially to the genus *Synchaeta*, it is usually impossible to determine species from contracted specimens, and often, when the animal is very transparent and lying amongst flocculent debris, etc., it is very difficult to distinguish it as a rotifer at all. When located, however, and after careful note has been taken of external appearances, it is often necessary to kill the animal and dissolve out the jaws or trophi with a solution of sodium or potassium hydroxide. Samples were first examined in a glass dish under the low power of a dissecting microscope, and individual specimens transferred with a fine pipette to a Rousselet compressorium for detailed study. All drawings were made from living specimens while held still in the compressorium, the method of drawing being that described by the writer (Hollowday, 1946).

Synchaeta triophthalma Lauterborn (Fig. 1 A, B).

Lauterborn, R., 1894. *Wiss. Meeresunters. Biol. Anst., Abt. Helgoland*, Bd. pp. 207-13, fig. 1.

S. triophthalma was originally found in 1893 by Dr Lauterborn off the coast of Heligoland, and subsequently by John Hood in the sea off Dundee. A brackish-water species, it has now been recorded from the Bay of Naples, Trieste, the Skagerak, Bergen, Liverpool and the Cheshire coast, where it is found in rock pools on Hilbre Island. It has recently also been recorded from New Zealand, in Oamuru Harbour.

At Plymouth it occurred in Stonehouse Lake, a tidal creek opening on Plymouth Sound between Plymouth and Devonport. It is quite probable that this species is common in brackish situations all round our coasts.

It occurred at Plymouth in April 1946, only female specimens being observed, and most of these carried eggs. As far as the writer is aware, the male is as yet unknown. The eggs carried by these Stonehouse specimens were of the ordinary, parthenogenetic type. According to Rousselet, *S. triophthalma* dies almost immediately if placed in fresh water, but, on the other hand, it never seems to occur in water of a very high salinity, preferring rock pools above the highwater mark, or in the 'splash' or 'spray zone', or the upper reaches of creeks and river estuaries. It was never observed in the Hamoaze or the Sound.

S. triophthalma is fairly easy to recognize, being extremely wide anteriorly, possessing, as a rule, three main pigment spots. A rather unique feature is the asymmetrical left lateral antenna, situated, not in the usual position (the lumbar region), but on a prominent swelling on the left dorso-lateral surface of the foot. According to Rousselet, the right lateral antenna is absent, but the writer has recently been informed by Mr A. L. Galliford that Remane has found what he believes to be the right lateral antenna in the normal position, but very inconspicuous, and without the brush of sensory setae. Nothing was seen of this in the Plymouth specimens.

The foot terminates in a single pointed toe (Fig. 1B).

Synchaeta littoralis Rousselet (Fig. 1C).

Rousselet, C., 1902. *Journ. Micr. Soc.*, p. 398, pl. vii, fig. 15.

While apparently a rare rotifer in Plymouth Sound and the Hamoaze, this species is reported common in brackish water at Leasowe, Cheshire, by Mr Galliford, and the accompanying illustration was drawn from a Leasowe specimen. It has been observed only once or twice at Plymouth, occurring in one tow-net samples collected by the motor boat *Gammarus* between Drake's Island and the Hoe in May and June 1947.

The size of this species seems rather variable. Rousselet gives the maximum length as 238 μ . The specimen here depicted, and most of the other Leasowe specimens measured 192 μ or thereabouts, and the Plymouth Sound specimens agreed with this.

The body is stouter than in *S. triophthalma*, being more cylindrical in shape. There are two streams of purple granules connecting the frontal eye-spots with the occipital. The lateral antennae are placed some three-quarters of the way down towards the foot, at the point where the trunk begins to narrow. No males were observed at Plymouth.

Originally described by Rousselet from specimens collected at Dundee by Good, it has been found at Great Yarmouth, Margate and Leasowe, Cheshire. There is a doubtful record for Naples.

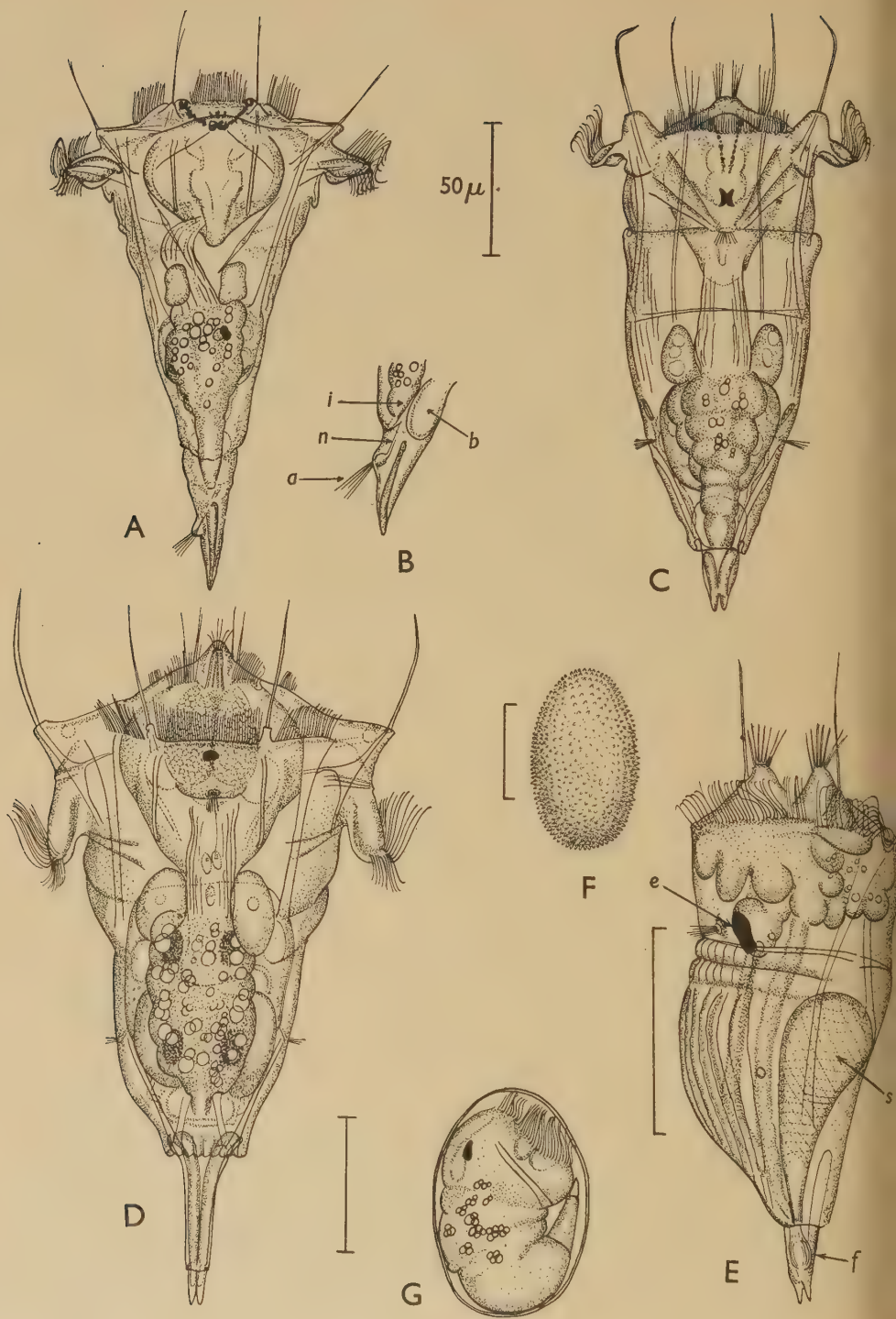


Fig. 1.

Synchaeta vorax Rousselet (Fig. 1D-G, 2A).

Rousselet, C., 1902. *Journ. R. Micr. Soc.*, pp. 408-10, pl. viii, fig. 19.

This species has been more thoroughly investigated by the writer at Plymouth than any other rotifer. It is not only common in the inshore waters of the Sound, but occurs also beyond the breakwater for considerable distances. Its presence in large numbers in all fine tow-net collections, during the summer months, must have been noticed by many workers studying fresh plankton samples at Plymouth. It is probably this species which Lebour records 'occasionally in tow-nets from the Sound' (Marine Biological Association, 1931, p. 149).

Occurrence and swarming periods at Plymouth

S. vorax was numerous in the first plankton samples collected by the writer from a rowing boat beyond Drake's Island in April 1946. Fig. 1D was drawn from a specimen in this first collection. It subsequently occurred in samples collected by the laboratory boat beyond the breakwater, although somewhat sparingly. Owing to the writer's preoccupation with other groups, no further records were made during 1946, but this was doubtless due to the fact that only medium tow-net samples were examined. During 1947, however, the rotifer was closely studied from February until its climax and sudden disappearance in May. Owing to extremely adverse weather conditions early in the year, no collections were made before February, so it is not possible to say exactly when it reappears from the previous summer's resting eggs. It was present in very small numbers during February, increasing steadily throughout March and April, and by the middle of May it was, on several occasions, easily the most numerous member of the zooplankton in fine tow-net collections. Mr P. S. B. Digby informed the writer about this time, that he had recently found it very numerous while studying copepods from the Sound.

About the time that *S. vorax* reached its climax, in the middle of May, there appeared in the Sound great quantities of the alga *Phaeocystis poucheti* Grangerh., and it was a common sight to see many *Synchaeta vorax* madly swimming away with their protruded unci at the cells round the outer margins of

Fig. 1. A, *Synchaeta triophthalma* Lauterborn; ♀ from Stonehouse Lake, Plymouth; length 190 μ ; dorsal aspect. B, the same, enlarged lateral aspect of 'foot'. C, *S. littoralis* Rousselet; ♀ from Leasowe, Cheshire; length 192 μ ; dorsal aspect. D, *S. vorax* Rousselet; ♀ from Plymouth Sound, Apr. 1946; length, with foot extended, 250 μ . E, the same; ♂ from Plymouth Sound, May 1947, showing the 'foot' extended; length 129 μ ; left dorso-lateral aspect. F, the same, resting egg deposited in *Phaeocystis*, Plymouth Sound, May 1947; length 93 μ . G, the same, developing egg showing ♂ shortly due to hatch, length 84 μ . a, antenna; b, bladder; e, eye spot; f, foot; i, intestine; n, nerve; s, sperm sac. Vertical scales all represent lengths of 50 μ .

the colonies. This went on for over a week, and then males appeared in large numbers. It must be noted that the writer never actually witnessed copulation, which is usually a necessary observation before deciding on the identity of most male rotifers, but these males agreed in most respects with the details given by Rousselet; furthermore, there were no females of any other species of *Synchaeta* present at the time, and almost immediately after these males appeared, the *S. vorax* began to lay resting eggs (a result of fertilization), these being deposited in the gelatinous masses of the *Phaeocystis*. The rotifer disappeared with a suddenness quite common in plankton rotifers; samples collected on 23 May 1947 being entirely devoid of a single active specimen, although many resting eggs still remained in the masses of *Phaeocystis*.

For over a year after first collecting this species at Plymouth, the writer was undecided as to its specific identity, and although the final decision was agreed to by Mr Galliford (who has studied the species fairly extensively at Liverpool), after much discussion and detailed study of all available literature, drawings, and Rousselet's own mounted specimens, there are one or two points wherein the Plymouth specimens differ from Rousselet's original published description and the accompanying figures.

First of all, it would appear that there are two distinct forms of *Synchaeta vorax* differing in the size of the whole animal, and in the proportions of the foot. In all other respects, these two forms are identical. The Plymouth specimens all measured an average of $250\ \mu$, being possessed of a long slender foot. This size compares well with the average of $272\ \mu$ given in the original description, and the $238\ \mu$ which is the greatest length of some specimens mounted by Rousselet himself in 1899 and recently examined by the writer. At Southport and Liverpool, however, Mr Galliford finds a smaller form which has a somewhat stouter foot than those at Plymouth, being more in keeping with the original description and drawing in this respect, but measuring only $200\ \mu$. Another slide mounted by Rousselet, and lodged at the Manchester University, shows specimens with a fairly stout foot and a total length which varies from $196\ \mu$ to $216\ \mu$.

Another slight difference in the Plymouth specimens was their apparent 'calmness', which is certainly not in keeping with the wild, voracious habits ascribed to the species by Rousselet, and faithfully exhibited by the specimens from the Lancashire coast. Indeed, Rousselet had good reasons for adopting the specific name *vorax*, and in his original description he says: 'the species swims with such impetuosity through the water that its rush cannot be described otherwise than furious; its course is straight forward, then it dashes suddenly round in another direction, attacking any other *Synchaeta* that may come in its way, and not at all particular as to species. I have seen it seize an unfortunate *S. triophthalma* with its jaws, carry it in its mouth and devour it without a moment's stop in its furious career. No other *Synchaeta* of my acquaintance is so fast in motion and so fierce of temper.'

The Plymouth specimens seemed placid enough, though swimming fairly rapidly in spirals, but were never observed to attack other small organisms, or their own kind. Fierce nibbling attacks were, however, made on the *Phaeocystis* already mentioned.

The males, which appeared in numbers during the middle of May, were little smaller than the $149\ \mu$ specified by Rousselet, and the majority averaged $25\ \mu$. Like most other male rotifers, the males of this genus are devoid of digestive system, but possess a well-developed genito-urinary system. Most of the body cavity is occupied by the large sperm sac which opens into a small protuberance on the dorsal surface of the foot, forming a rudimentary penis. The movements of the male are even more vigorous and rapid than those of the female.

A final perplexing point regarding this species may be mentioned. Although the two frontal coronal prominences of the male, each with its crown of setae, were plainly visible (these are stated by Rousselet to be peculiar to the male of *Synchaeta vorax*), the three small tubular frontal antennae, also a characteristic feature of this male, could not be found.

The resting egg has an opaque shell, beset with many small pointed protuberances, and measures about $93\ \mu$ in length (Fig. 1 G).

S. vorax appears to have a wide distribution, but it is quite probable, in view of the cosmopolitan habits of many rotifers, that further investigation of marine and brackish rotatorian faunas in foreign parts will reveal that many of the rotifers occurring round our coasts have a world-wide distribution. To date, *S. vorax* has been recorded from Dundee, Liverpool, Southport, Bergen, Lake Ladoga (fresh water), and the Suez canal.¹

As in fresh water, planktonic rotifers in the sea doubtless become the prey of fish fry, but it would appear they also figure in the diet of other pelagic vertebrates, and *S. vorax* has been observed being devoured by Hydro-medusae at Plymouth and also at Southport (Hollowday 1947).

Encentrum marinum (Dujardin) (Fig. 2 B, C)

Encentrum marina Dujardin, 1841. *Histoire naturelle des Zoophytes* etc., p. 649, pl. 22, fig. 4.

Distemma marina Gosse, 1887. *Journ. R. Micr. Soc.*, 1887, p. 367. (Not *Distemma marinum* Ehr.)

Distemma platyceps Gosse, P. H., 1887. *Journ. R. Micr. Soc.*, 1887, p. 866, pl. 14, fig. 12.

Neurotrocha marina Bergendal, D., 1892. *Acta Univ. Lundensis*, Vol. 28, No. 4, p. 50, pl. 1, fig. 13.

Stilena marina N. von Hofsten, 1912. *Marine, Litorale Rotatorien* etc. *Zool. Bidr. Uppsala*, Vol. 1, p. 203.

¹ Since this report was compiled, it has been found in brackish water at West Mersea, Essex, by A. L. Galliford and C. Rudlin.

A strictly littoral-zone species, occurring in masses of algae in rock pools and brackish pools above the high-tide mark. It is also capable of living in fresh water as well as water of oceanic salinity.

The general appearance of the rotifer can be observed in the accompanying drawing, made from a rock pool specimen collected along the shores of Barn Pool and Mount Edgcumbe. It is doubtless common all round the shores of the Sound, although specimens were observed only in the above-mentioned region.

E. marinum has been recorded from Naples, Jacobshaven, Helsingfors, Bergen, Liverpool, and the Firth of Tay, also in salt and brackish water at Atlantic City, New Jersey, and Mount Desert Island, Maine. In fresh water, Royal Botanic Gardens, Regent's Park.

Several members of this genus are known to occur in salt pools and brackish waters.

Proales reinhardti (Ehrenberg) (Fig. 2D, E)

Furcularia reinhardti Ehrenberg, 1833. *Abh. Akad. wiss. Berlin*, p. 208.

Distemma marinum Ehrenberg, 1838. *Infusionsth.*, p. 450, pl. 56, fig. 4. (Not *Distemma marina* Gosse.)

Mytilia tavina Hudson, C. T. & Gosse, P. H., 1886. *The Rotifera*, Vol. 2, p. 110, pl. 26, fig. 8.

M. teresa Gosse, P. H., 1887. *Journ. R. Micr. Soc.*, p. 3, pl. 1, fig. 7.

Notommata theodora Gosse, 1887. *Journ. R. Micr. Soc.*, p. 862, pl. 14, fig. 2.

Mytilia poecilops Gosse, 1887. *Journ. R. Micr. Soc.*, p. 869, pl. 15, fig. 21.

M. producta Gosse, 1887. *Journ. R. Micr. Soc.*, p. 870, pl. 15, fig. 22.

Notommata reinhardti Hudson & Gosse, 1889. *The Rotifera*. Suppl., p. 22.

Diops marina Bergendal, D., 1892. *Acta. Univ. Lundensis*, Vol. 28, No. 4, p. 83, pls. 4, 5, fig. 27.

Pleurotrocha reinhardti von Hofsten, 1912. *Zool. Bidr. Uppsala*, Vol. 1, p. 187, fig. 1.

Proales reinhardti Harring, H. K. & Myers, F., 1924. *Rotifera of Wisconsin*. II. *Trans. Wis. Acad. Sci. Arts, Let.*, p. 431, pl. XVI, figs. 6-10.

Few rotifers have been described so many times under different names by the same author as the one now known as *Proales reinhardti* (Ehrenberg).

A littoral, browsing species, *P. reinhardti* is common in rock pools, and in masses of *Fucus*.

All the main characteristics of the rotifer are so clearly shown in the accompanying illustrations drawn from Plymouth specimens, that little comment

Fig. 2. A, *Synchaeta vorax* Rousselet; ♂, from Plymouth Sound, May 1947, with foot and penis withdrawn; length 124 μ ; left dorso-lateral aspect (cf. Fig. 1E). B, *Encentrum marinum* (Dujardin); ♀, from rock pool, Mount Edgcumbe, Plymouth, with trophi (*t*) protruded for browsing; length c. 165 μ ; right lateral aspect. C, the same, enlarged view of the trophi. D, *Proales reinhardti* (Ehrenberg); ♀, from rock pool, Jennycliff, Plymouth; length 260 μ ; left lateral aspect. E, the same, ♀ from rock pool, Mount Edgcumbe, Plymouth; dorsal aspect. F, *Trichocerca marina* (Daday), ♀ from the plankton, Plymouth Sound; body length 150 μ ; left lateral aspect. *d*, ingested diatoms; *e*, eye spot; *f*, foot; *g*, gastric gland; *r.c.*, renal canal; *r.s.*, retrocerebral sac; *s*, sperm sac; *t*, trophi; *v*, vitellarium. Vertical scales (different for each drawing) all represent lengths of 50 μ .



Fig. 2.

is required here regarding its anatomy. It not infrequently swallows large diatoms, and it is indeed quite difficult to imagine how the specimen here depicted managed to swallow those shown in its stomach. The pedal glands are very long, and open into the toes by fine ducts.

Proales reinhardti is probably common all round our coast, Gosse recorded it from Oddicombe Point, Devon, also from Torbay, and tide-pools at Invergowrie. The writer has found it along the Cheshire coast, at Hilbre Island and at Leasowe, also in *Fucus* in rock pools at Bexhill-on-Sea, Sussex.

It is also reported from salt and brackish water at Copenhagen, Reval, Helsingfors, Wiborg, Hapsal, Bergen and Naples, and from brackish tidal pools at Atlantic City.

At Plymouth it is numerous at Jenny Cliff, Rum Bay, Barn Pool and Cremyl.

Trichocerca marina (Daday) (Fig. 2F)

Diurella marina Daday, 1890. *Ert. Termi. Kör.*, Vol. 19, No. 17, p. 16, pl. 1, figs. 23, 9 and 10.

Mastigocerca dubia Lauterborn, 1894. *Wiss. Meeresunters.* N.S., Vol. 1, p. 213, fig. 2.

Rattulus dubius Jennings, 1902. *Bull. U.S. Fish. Comm.*, Vol. 22, p. 340, pl. 14, fig. 133.

R. henseni Zelinka, 1907. *Rotatoria Plankton-Exposit.*, p. 19, pl. 2, figs. 1-7.

R. marinus De Beauchamp, 1907. *Bull. Soc. Zool. France*, Vol. 32, p. 148.

Of the rotifers found at Plymouth this species is the only one which can be termed truly marine and oceanic. It was first noticed by the writer in coarse tow-net samples from the Sound in the summer of 1946, when it was observed swimming amongst medusae of *Obelia* sp. It is rather a small rotifer, however, and requires a fine net to collect it as a rule. It was not seen again until May 1947, and occurred very sparingly in samples throughout June, after which all observations were discontinued.

Specimens varied in size; most measured just over 150μ including the single foot spine, but the specimen depicted was somewhat larger. The members of this genus are remarkable for their asymmetrical trophi, which are adapted for suction, and for the asymmetry of the toes. In many species one toe only is left, usually as a long spine, as in *Trichocerca marina*, while in other members of the genus, the other toe is greatly reduced or very rudimentary. The front of the lorica, i.e. that part covering the head, is usually rather flexible, but that of *T. marina* appears even more so than in the various fresh-water species with which the writer is familiar. On retraction of the head it can be drawn to a close like the mouth of a sack.

This species was collected by the German Plankton Expedition of 1895 (Zelinka, 1907) from various stations in the Atlantic, being most numerous near the coast of Greenland. There seem to be very few records of its distribution; Mr Galliford reports it from the Lancashire coast.

THE PLYMOUTH ROTATORIAN FAUNA COMPARED WITH THAT OF LIVERPOOL

It must be admitted that the writer was somewhat disappointed at the apparent poverty of the Plymouth rotatorian fauna as compared with that of Liverpool and neighbouring stations along the Lancashire and Cheshire Coast, reported by Galliford (1945, 1946), although, as previously remarked, further investigation at Plymouth would probably add several species to the present list. Compared with the six species found at Plymouth, Galliford has recorded no less than thirty-five species as occurring in salt and brackish waters at Liverpool. Although no figures are available for comparison, degree of salinity may be a controlling factor, and it is hoped that further details regarding the comparative salinity of the Plymouth and Liverpool habitats will be assembled in due course, but it is here vitally necessary to stress certain facts regarding the application of the term 'marine' to the rotifers occurring round our coasts, as well as in continental coastal waters in general.

It is probably a little premature at this stage of our knowledge to make broad generalizations on the distribution of coastal Rotifera, for so little collecting has yet been done, but it is noticeable that most of the species referred to by various workers as 'marine rotifers' are in fact confined to estuarine waters of low salinity, being more numerous in the upper reaches of creeks and in 'marine lakes', such as that at Southport, which is occasionally replenished from the sea, but which is constantly having the salinity lowered by rain. Pools above high-water mark which receive spray and rain are also favourite haunts of these brackish rotifers. The extensive analytical details given by Zelinka (1907) are apt to be misleading, for many of his salt-water records are really from brackish habitats, and should be considered with caution. Although *Synchaeta vorax* and *S. littoralis* have been found in the open waters of the Sound, the Sound itself, like Liverpool Bay, and the various other stations at which coastal rotifers have been studied in these islands, has numerous sources of fresh water emptying into it. At Bexhill-on-Sea, Sussex, where there are no rivers close at hand, extensive collecting with hand-net and tow-net, inshore and on the open sea, revealed no rotifers whatsoever, although *Proales reinhardti* occurred in *Fucus* in rock pools. One single specimen of *Synchaeta*, contracted and otherwise unrecognizable, was taken in the incoming tide.

Certain rotifers however, among them *Proales reinhardti* and *Encentrum marinum*, appear to inhabit salt, brackish, and fresh-water habitats, although it is not known whether individuals are capable of withstanding transfer from one habitat to the other. That both species are found in all three situations however, is quite certain. Some of the brackish species seem very susceptible to osmotic changes; thus Rousselet (1902) records that *Synchaeta triophthalma* quickly succumbs on immersion in fresh water. On the other hand, it does not appear to favour waters of high salinity.

As to the seasonal appearances, life histories, and general ecology of these coastal rotifers, little or nothing is known, and the field presents many interesting problems worthy of further investigation.

SUMMARY

Six species of rotifer, including one oceanic species and representing four genera, are recorded for the first time from Plymouth. Remarks are made on various interesting features of their anatomy, details are given of their times of occurrence at Plymouth, with notes on their location and known distribution in other parts of the British Isles, and in foreign waters.

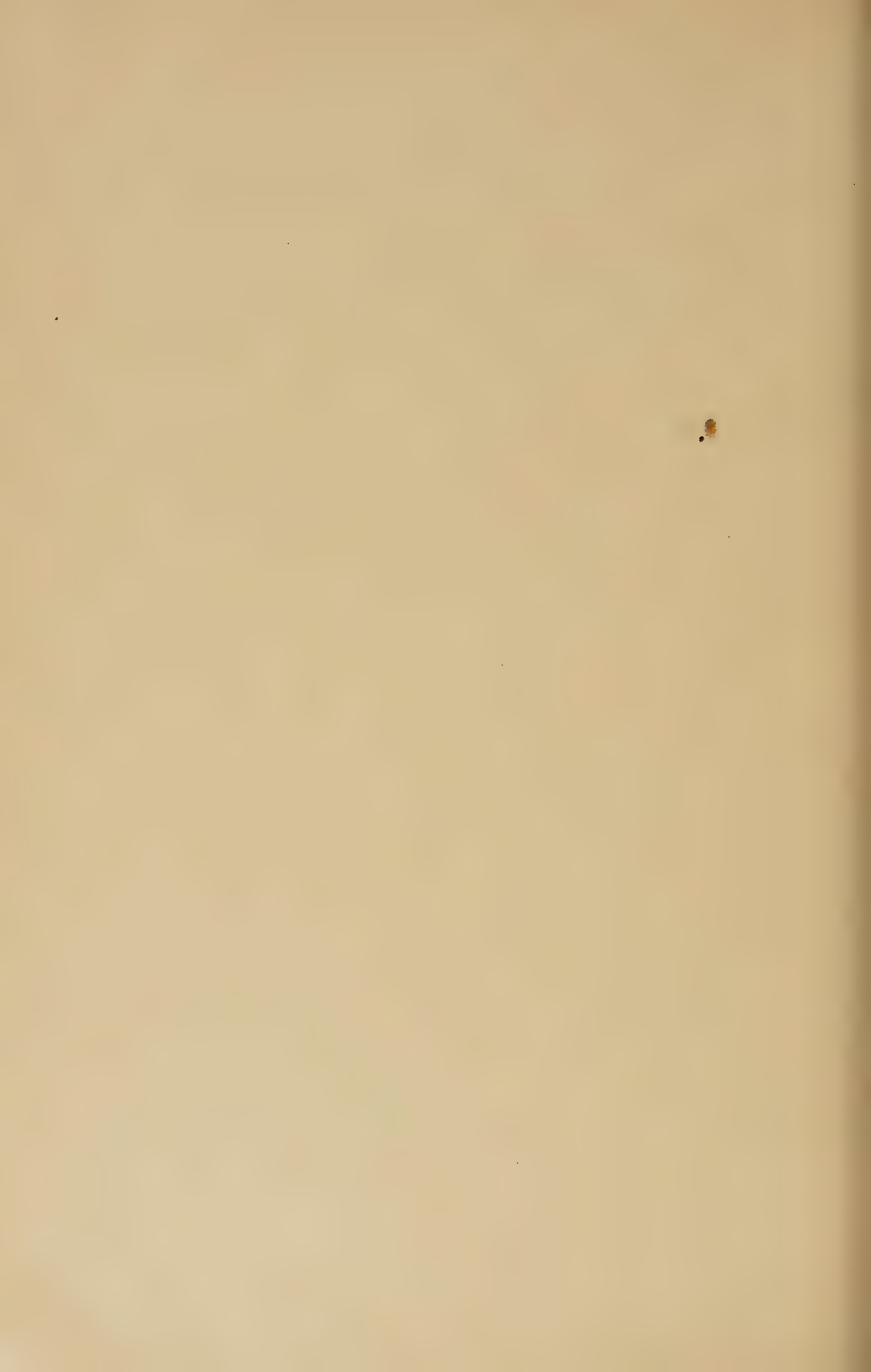
Attention is called to the apparent poverty of the Plymouth marine and brackish-water Rotifera as compared with that of Liverpool, investigated at length by Galliford. It is stressed that no exact conclusions as to the reason for this can be made until after a more exhaustive survey, as some likely habitats adjacent to the Sound were not investigated. Attention is also called to the caution which must be exercised in terming rotifers marine, as most of those collected in coastal waters appear at present to be confined to areas where a considerable amount of fresh water is discharged into the sea. At least two species, one of which occurs in the Sound in May, are known to be truly oceanic, having been found in mid-Atlantic.

It is suggested that 'brackish' and 'estuarine' are the terms most applicable to the majority of coastal rotifers in the present state of our knowledge.

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STUDIES ON MARINE FLAGELLATES

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(Plates I and II, and Text-figs. 1-73)

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INTRODUCTION

During the years 1935 to 1940 experimental work was carried out at the Port Erin Marine Biological Station on the rearing of the larvae of the European oyster, *Ostrea edulis* L. At first, algal zooids and the naturally occurring microplankton in the sea water were used as sources of food for the larvae, but later the larvae were fed on pure cultures of flagellates with much more successful results (Bruce, Knight & Parke, 1940).

Six of the flagellates used in the experiments are here described. Three were isolated by Dr F. Gross at the Plymouth Laboratory (temporary labels 'B', 'C' and 'H', Gross) and three were isolated at Port Erin (temporary labels 'D', 'E' and 'I', Parke). Cultures of four of these flagellates are still maintained at the Plymouth Laboratory but the cultures of 'C' and 'H' were lost in 1941 when the laboratory was damaged.

ACKNOWLEDGEMENTS

My most sincere thanks are due to Prof. F. E. Fritsch and Prof. E. G. Pringsheim for their helpful criticism of part of the work. I am most grateful also to Mr W. M. S. Russell, who translated my descriptions of the organisms into Latin and who suggested the name *Dicrateria* for one of the new genera.

CHLOROPHYCEAE

POLYBLEPHARIDACEAE

Pyramimonas Schmarda

P. grossii n.sp. (Flagellate 'H', Gross.)

(Pl. II, figs. 17, 18; Text-figs. 1-12.)

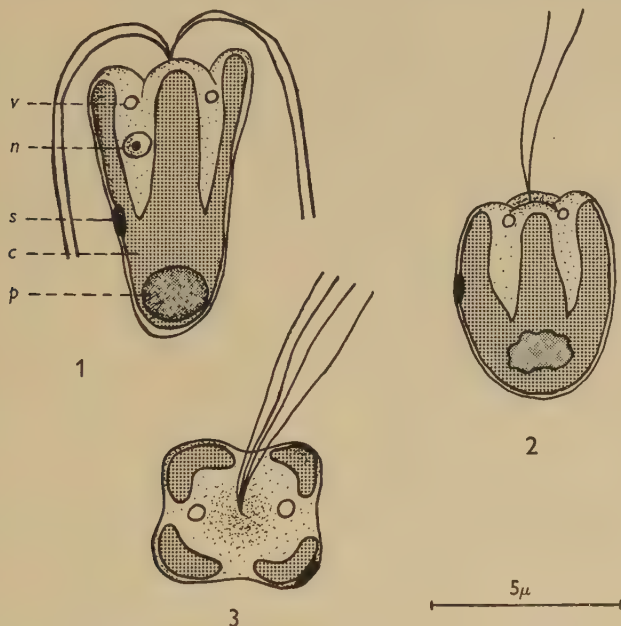
Cellula parva, pyramidiformi plerumque ac 4 lobis distinctis anterioribus praedita; quae transverse secta nisi ad apicem extremum formam praebet circularem; forma mutabili; 4 flagellis longitudine cellulae fere paribus in depressione mediocriter tenui ad apicem insertis; chromatophoro luteo viridi caliciformi cum 4 lobis anterioribus in margine dispositis et magno pyrenoide basali; amyli capsula pyrenoidi circumdata conspicua; stigmatibus singulis, mediano plerumque, rarius anteriore; nucleo anteriore plerumque ac laterali; 2 vacuolis ad apicem sitis, haud contractilibus; cellula $5.5-8\mu$ longa, lata $4.5-5.5\mu$. Ab nomine Doctoris F. Gross appellata, per quem segregata est.

This species was isolated by Dr F. Gross from a plankton sample taken from the sea water off Plymouth. In his records the first culture of 'H' was dated April 1936.

This species is normally inversely pyramidal, sharply truncate and four-lobed at the anterior end and somewhat tapering towards the posterior region (Text-fig. 1). As the periplast admits of extensive change of shape, transitions to shorter more or less cordate forms are frequent and longer, more subcylindrical forms also occur (Pl. II, figs. 17, 18). The lobes are confined to the anterior end of the cell and are continued backwards as ridges for only a short distance, so that an individual is circular in transverse section except at the extreme apex. Here the swelling of the lobes gives a transverse section the appearance of a square which has had the corners rounded and the sides indented (Text-fig. 3).

The anterior lobes surround a fairly shallow depression, from the centre of which arise four flagella, all originating from one point. The flagella are equal to, or slightly longer than, the length of the cell. No difference in the appearance of the four flagella could be detected when the staining methods of Loeffler (1889) and Fischer (1894) were used. The four are equal in length and thickness, and show no tapering towards the free end, but end quite bluntly. Movement of the organism is spasmodic and extremely rapid, but the organism can remain constant in direction for relatively long periods.

The chloroplast, bright yellowish green in colour, is cup-shaped with the sides deeply cleft into four lobes (Pl. II, figs. 17, 18). The thickened basal part of the chloroplast, behind the lobes, fills the posterior third of the body, occupying the whole periphery of the cell. It has a smooth outline since no posterior lobes or indentations are developed. Each lobe of the chloroplast passes forwards into one of the body lobes and is smooth at the apex, not indented. A large pyrenoid is situated in the thickened posterior portion of



Text-figs. 1-3. ($\times 5000$.) *Pyramimonas grossii* n.sp. 1. Normal shape of young motile stage, side view. c, chloroplast; n, nucleus; p, pyrenoid; s, stigma; v, vacuole. 2. Biflagellate stage, side view. 3. Young motile stage viewed from anterior end.

the chloroplast below the fusion of the lobes, usually at the extreme posterior end of the cell (Text-fig. 1). The pyrenoid is surrounded by a well-developed starch sheath.

A bright red stigma, projecting slightly above the general surface of the organism, is usually median in position (Text-fig. 1), but has frequently been observed at the extreme anterior end on a line with two non-contractile vacuoles which occur in the general cytoplasm within the chloroplast. The nucleus is visible in the living individual and is situated anteriorly in the body at a lateral position (Text-fig. 1).

Approximately 10% of the motile stages in a culture possess only two flagella. These individuals are smaller ($4-5\mu$) than the individuals with four flagella and practically spheroidal in shape with the anterior lobes less well developed (Text-fig. 2). The nature and function of the biflagellate individuals

have not been determined but, as Pascher (1927) has suggested for other genera, they may possibly be the 'basic' form, and the more frequent individuals with four flagella can then be regarded as double cells resulting from the early multiplication of the flagella prior to division. Fusion of the bi-flagellate individuals was never observed.

The motile individuals are very strongly phototactic and therefore tend to collect on one side of the culture flask. Here they readily assume the 'palmella-state'; the flagella are lost and the cells become spheroidal, developing a thin hyaline gelatinous envelope measuring $6-8\mu$ in diameter (Text-fig. 11). When numerous cells become aggregated together they become very irregular in shape. The outline of the chloroplast becomes indistinct but the stigma and pyrenoid persist and the vacuoles become more apparent, the latter frequently increasing in number.

Asexual reproduction is most frequent in the motile individuals, but it occurs also in non-motile cells (Text-fig. 10), and in individuals in the palmella-stage (Text-fig. 12). In the motile individuals it takes place by simple division along a longitudinal plane. When about to divide the cells increase in breadth; at the same time the pyrenoid shows signs of elongation transverse to the cell axis (Text-fig. 4). The pyrenoid then divides into two parts, the number of vacuoles is doubled and a second stigma develops. The nucleus then divides and the four lobes of the chloroplast divide by the splitting of each lobe (Text-fig. 5). Occasionally the nucleus divides before the pyrenoid.

In the majority the flagella separate as the cell broadens, two to each daughter-cell; two new flagella are then developed by each daughter-cell as division proceeds. Sometimes individuals bear eight flagella before the pyrenoid has divided.

The line of division passes through the thickened posterior portion of the chloroplast so that each part has one complete, now divided into two, and two half lobes of the original chloroplast (Text-fig. 6). In *P. delicatulus* Griffiths two complete lobes pass to each daughter-cell. Separation of the two daughter-cells takes place by gradual constriction, starting simultaneously at both the anterior and posterior ends of the individual but advancing more rapidly from the posterior pole (Text-fig. 7). The periplast divides simultaneously with the rest of the protoplast and is gradually completed on adjacent surfaces of the new individuals. The daughter-cells are commonly of unequal size.

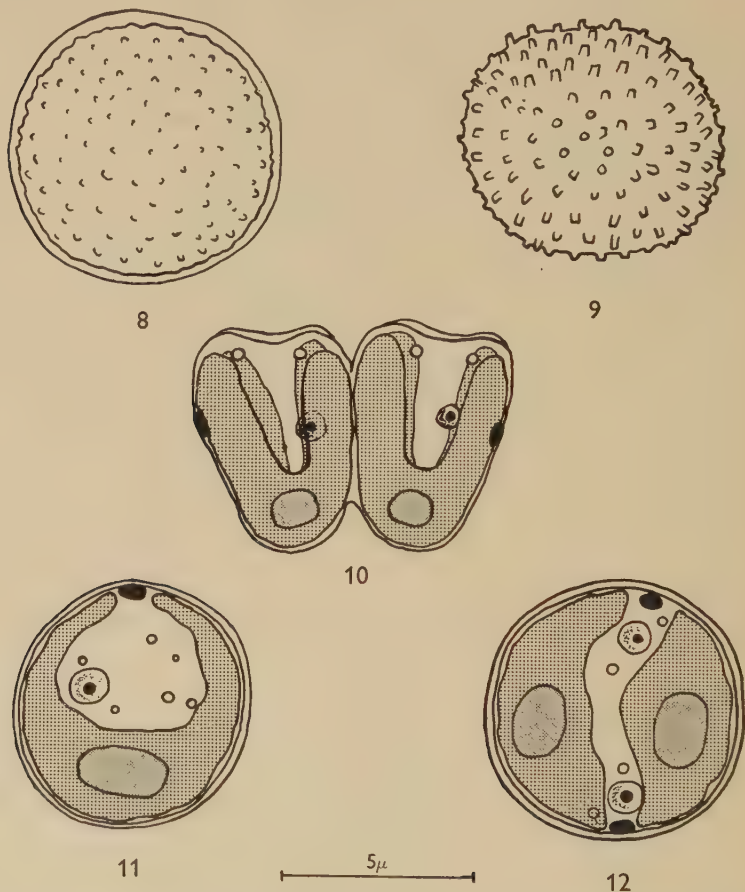
Hypnospores or cysts have been observed in the cultures (Text-figs. 8, 9). They are formed either from ordinary motile cells after the flagella have been withdrawn or from individuals already in the palmelloid phase. The cysts are usually spheroidal in shape, sculptured externally and measure $6-7\mu$ in diameter. The release of the contents of the cysts has not been observed.

From the marine species so far described, *P. adriaticus* Schiller (1913), *P. oltmannsi* Schiller and *P. impressus* Schiller (1925), *P. grossii* differs both



1. figs. 4-7. ($\times 5000$.) *Pyramimonas grossii* n.sp. 4. Large motile stage just prior to division, side view. 5. Early division stage of motile individual, side view. 6. Later division stage of motile individual, side view. 7. Two daughter-cells just prior to separation, side view.

in shape and in possessing a pyrenoid. It differs also from the brackish-water forms *P. obovata* Carter, *P. olivacea* Carter and *P. angulata* Carter (1937) in shape, in colour, in possessing a starch sheath around the pyrenoid instead of two saucer-shaped starch grains, and in the absence of longitudinal series of



Text-figs. 8-12. ($\times 5000$.) *Pyramimonas grossii* n.sp. 8. Early stage in cyst formation. 9. Mature cyst. 10. Fission in non-motile stage, side view. 11. Individual in palmelloid phase. 12. Early stage in fission in palmelloid phase.

minute puncta on the periplast. From the brackish-water *P. octociliata* Carter (1937) *P. grossii* differs in shape, colour, number of flagella, in possessing a stigma and in lacking puncta on the periplast. *P. grossii* also differs in shape and size from the six species described by Pascher (1932).

It differs also from *P. utrajectina* Bretschneider (1925) and *P. ovalis* Conrad (1930a) in size, shape, development of the anterior lobes, and in the size, shape and position of the stigma. *P. botryodes* Jane (1944) is clearly distin-

ished from *P. grossii* by the rounded prominences on the surface of the cell and by the shape of the chloroplast.

P. grossii is somewhat similar in shape to *P. tetra-rhynchus* Schmarda (1850), *P. delicatulus* Griffiths (1909), *P. inconstans* Hodgetts (1920), and *P. montana* Reiter (1925). From all these species, however, it differs in its smaller size. In addition, it differs from *P. tetra-rhynchus* in the number of the anterior incisions in the chloroplast, in the position of the stigma and in the absence of stroma starch grains. It lacks also the hollowing at the posterior end that occurs in *P. delicatulus* and possesses a stigma and vacuoles which are lacking in that species. *P. grossii* differs from *P. inconstans* in having a lobed chloroplast and in the degree of development of the body lobes. From *P. montana* it differs in colour, in the absence of stroma starch and also in the development of the apical lobes.

CHRYSTOPHYCEAE

CHROMULINACEAE

Chromulina Cienk.

pleiades n.sp. (Flagellate 'E', Parke.)

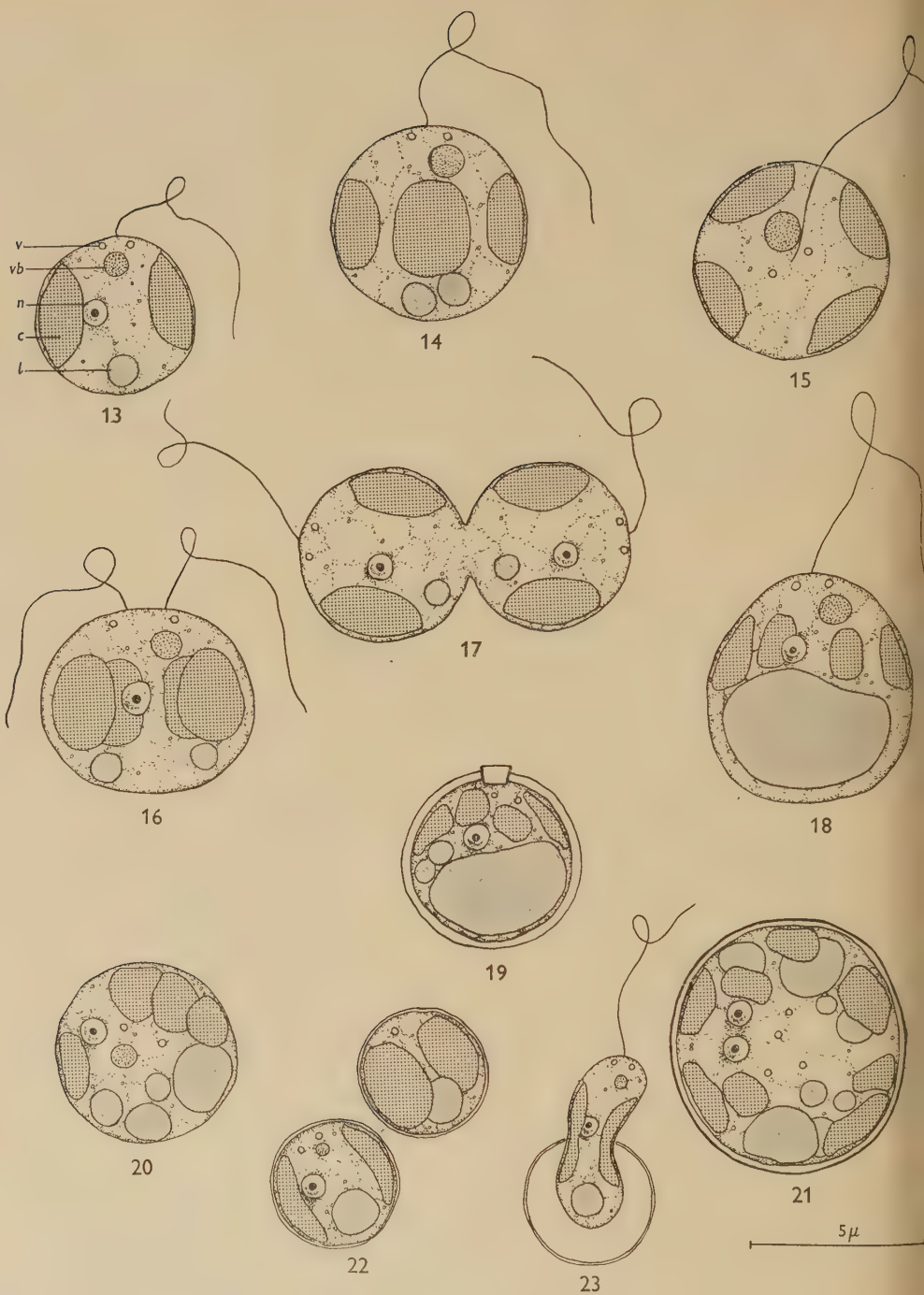
1. I, fig. 2; Text-figs. 13-23.)

Cellula parva, sphaeroidi, periplasto differentiae carente praedita; 2 chromatophoros cellulis recentibus, vetustioribus 4 praebentibus fulvos pallidos lateriformes; flagello singulo cellulae diametro 1.5-2 plo longiore; nucleo centrale; 2 vacuolis parvis haud contractilibus ubi insertum est flagellum repositis; 'vacuolo' bene definito cui granula insunt refringentia vibrantia in cellula mobili plerumque visendo prope polum illum ex quo existit flagellum; non sexu propagatur per gradus mobiles immobilesque; cystis sphaeroidibus ovatis cum membrana externa laevi; non deest multiplicationis genus melloidem per gradum effectae; cellulae mobili est diametros 3.5-6 μ ; stoma diametros 5-6 μ .

This species was isolated at Port Erin from 'outside' sea water in February 1939.

The individuals of this species are spheroidal and have an undifferentiated, smooth, firm periplast, which does not admit of any change of shape; they measure from 3.5 to 6 μ in diameter. The saucer-shaped chromatophores, pale golden-brown in colour, are parietal; two are present in the smaller individuals, but in the larger individuals four is the more usual number (Text-figs. 13, 14). There is a medium-sized nucleus situated more or less centrally in the body and one or more small masses of leucosin at the pole opposite to that from which the flagellum arises. As the individuals increase in size the amount of leucosin also increases until it fills nearly half the volume of the cell (Text-figs. 13, 14 and 18). No extrusion of the leucosin masses has been observed.

The flagellum, one and a half to twice the cell diameter in length, is delicate



Text-figs. 13-23. ($\times 5000$.) *Chromulina pleiades* n.sp. 13. Young motile stage, equatorial view. *c*, chromatophore; *l*, leucosin; *n*, nucleus; *v*, vacuole; *vb*, vibrating body. 14. Older motile stage, equatorial view. 15. Older motile stage, viewed from pole at which flagellum is inserted. 16. Early division stage of motile individual. 17. Later division stage of motile individual. 18. Older motile stage containing large leucosin mass. 19. Mature cyst, equatorial view. 20. Reproduction in the palmelloid phase, stage 1. 21. Reproduction in the palmelloid phase, stage 2. 22. Reproduction in the palmelloid phase, stage 5. 23. Reproduction in the palmelloid phase, stage 6.

and difficult to see in the living individuals; stained preparations show that it does not arise from a basal granule and that it tapers very slightly towards the free end. No evidence was obtained of the presence of fine cilia on the flagellum although Vlk (1938) records them in an unnamed species of *Chromulina*. This species moves smoothly and fairly slowly; it swims for comparatively short distances, or round in circles, and then has long periods of quiescence. Strong illumination tends to stop movement in a fairly short time.

Two small non-contractile vacuoles are present near the point of insertion of the flagellum. Another larger 'vacuole', or clearly delimited spheroidal body, is usually developed in the motile individuals near to the two small vacuoles (Text-figs. 13-15, 18). This well-defined structure is sometimes quite large and contains shining vibrating bodies. The movement of these bodies is very similar to that found in Desmids in the terminal vacuoles containing minute crystals of calcium sulphate. In addition to the Brownian movement of crystals, Chifflet & Gautier (1905) have shown that Brownian movement of cytoplasmic granules frequently occurs. They observed its occurrence in many species of *Spirogyra*, in *Haematococcus pluvialis* and in the dense protoplasm at the tips of the root hairs of *Azolla caroliniana*. In the last genus they found Brownian movement also in the vacuoles in the root hairs, but in the vacuoles the motile bodies, more numerous than in the protoplasm, were found to be crystals of calcium oxalate.

Carter (1937) records the presence of large numbers of minute granules in active Brownian movement in individuals of *Prymnesium parvum* and *P. minutum* Carter. In these species, however, the granules are in 'an ill-defined region', not a clearly defined one as in *Chromulina pleiades*, and are therefore most probably cytoplasmic granules. The sharp outline of this body in *C. pleiades* suggests that it is a vacuole and that the 'bodies', showing Brownian movement, are probably of a crystalline nature.

There are records in the literature of the occurrence, in members of the Chrysophyceae, of collections of strongly refractive particles having a crystalline appearance (Scherffel, 1911; Doflein, 1922, 1923). Scherffel (1911) observed them in *C. nebulosa* Cienk., in addition to other genera, and Doflein (1923) records them as being a distinctive feature of *C. minima* Doflein. Neither author refers to movement of the particles nor to their enclosure in a clearly defined 'body'. Korshikov (1929) refers to leucosin masses becoming, under pressure, vacuoles containing suspended particles in Brownian movement; he records, however, that these vacuoles have lost the former refraction power of the leucosin. They are therefore different in nature from the 'vacuoles' in *C. pleiades*.

Asexual reproduction takes place by simple fission, usually of the motile individuals, but sometimes of individuals which have either cast or withdrawn their flagellum. Division of the cells takes place in both the light and the

dark, and occurs in the normal way. The individual first broadens and a second flagellum develops close to the original one, usually before the division of the nucleus. Four chromatophores are usually present in the cell before division starts so that two pass to each daughter-cell. One of the small vacuoles passes to each cell and the second arises anew as the two cells start to separate. The vibrating 'vacuole' can be seen in the early division stages but not in the late stages as the two daughter-cells draw apart (Text-figs. 16, 17).

Cysts are produced in cultures which have been left for at least 3 months without subculturing. They develop inside large individuals which are nearly half-filled by leucosin. No gelatinous investment forms round the individuals. The cysts are spheroidal to very slightly ovoid in shape and measure $5-6\mu$ in diameter (Text-fig. 19). The outer surface of the cyst wall is smooth and the plug, which protrudes only slightly above the surface, has the shape of an inverted truncated cone.

In this species (Text-figs. 20-23), and in the three following species belonging to the Chrysophyceae, a form of reproduction takes place in a palmelloid phase which has so far not been recorded in the literature, unless Lund's description of the production of sporangia in *C. sporangifera* is a somewhat similar process (Lund, 1942). The stages that have been obtained so far in this palmelloid form of reproduction are described and discussed under the next genus, *Isochrysis*.

Chromulina pleiades differs from *C. microplankton* Pascher (1913), *C. parvula* Conrad (1930b) and *C. sphaerica* Doflein (1923) in possessing two chromatophores; it differs further from the first two in size and from the last, which is about the same size, in lacking pyrenoids and also in the length of the flagellum. *C. pleiades* resembles most closely *C. sphaeridia* Schiller (1929), but it is smaller in size, has a shorter flagellum and its vacuoles are not contractile. It differs also from all other species of *Chromulina* in possessing a 'vacuole' containing vibrating bodies.

ISOCHRYSIDACEAE

Isochrysis n.gen.

Cellula solitaria, natante, nuda, periplasto differentiae carente praedita; ellipsoidi, ad anteriorem partem truncata, ad posteriorem rotundata; dorsi-ventraliter paulum depressa; quae transverse secta formam praebet ovatam; forma mutabili; 2 flagellis, longitudine paribus, ad anteriorem partem existentibus; 2 chromatophoris magnis lateralibus fulvis; ocello parvo; nucleo parvo mediano; desunt vacuola; cellula pabulum holophytica; nec oleo nec leucosino indigente; sine sexu propagatur fissione in longitudinem effecta per gradus mobiles immobilesque; cysto intra cellulam confecto; cystis sphaeroidibus cum membrana externa paulum sculpta; non deest multiplicationis genus palmelloidem per gradum effectae.

I. galbana n.sp. (Flagellate 'I', Parke.)

Pl. I, figs. 4-10; Text-figs. 24-45.)

With the characters of the genus.

Motile cell: length, 5-6 μ ; breadth, 2-4 μ ; thickness, 2.5-3 μ .

Cyst diameter, 5-6 μ .

Isolated from sea water from one of the fish ponds at the Marine Biological Station, Port Erin, in January 1938.

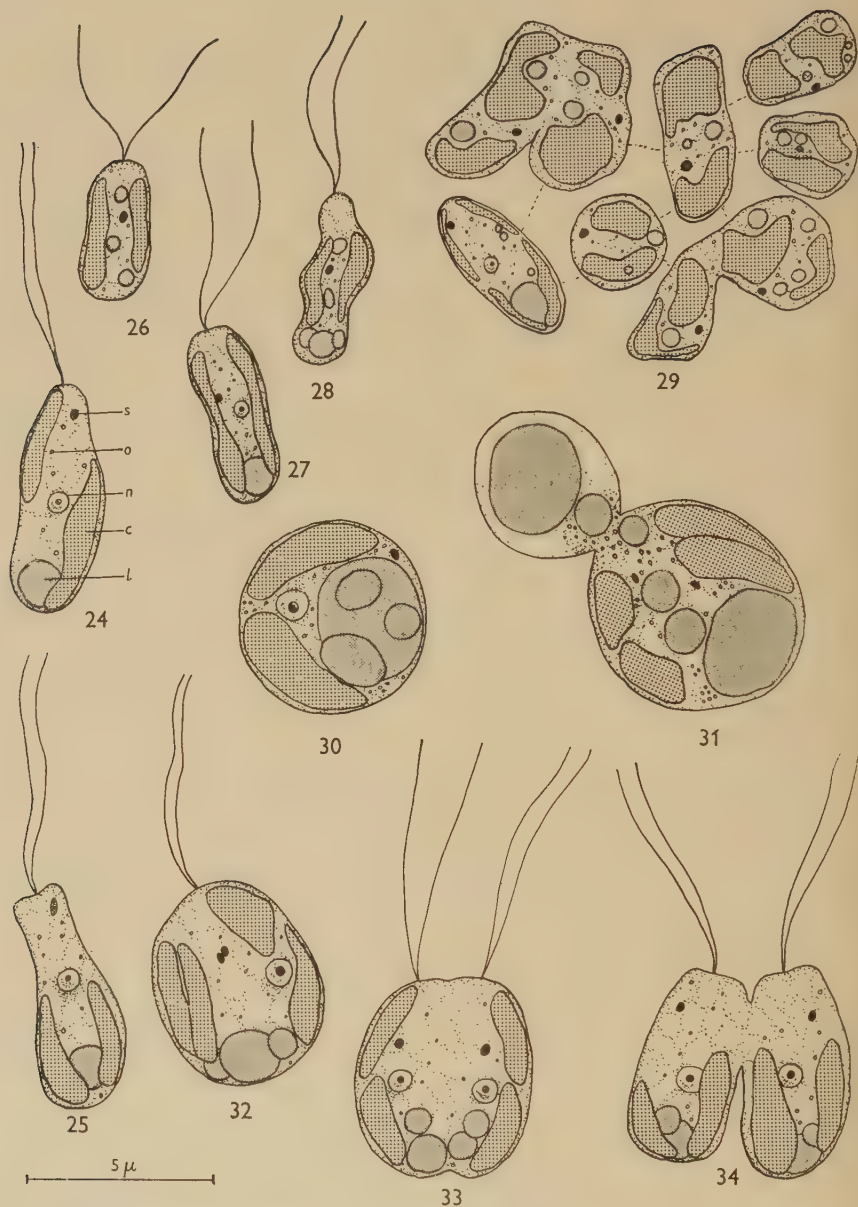
The actively motile individuals of this species are usually somewhat ellipsoidal, flattened anteriorly and rounded posteriorly, with a slight dorso-ventral flattening so that the cells appear oblong in side view (Pl. I, fig. 10), and ovoid in cross-section.

The capacity to change shape is a strong character of this species, and consequently variation in the shape of individuals is quite considerable (Pl. I, figs. 7, 10; Text-figs. 24-28).

Two equal flagella arise anteriorly, their length varying from once to twice that of the cell; they are fairly thick and can be seen quite easily in the living material; no basal granule is developed at their point of origin. Movement of the individuals, usually in a forward direction, is slow and steady with rotation of the body round the long axis. When the cells are at rest the flagella are stiff and lie away from the body, but when in motion they are out in front of the cell and carry out an undulating movement. This species shows a slight phototactic reaction.

The method of swimming of this species has been investigated by Lowndes (1943, pp. 101-2). He found that the organisms swam forward smoothly, rotating and gyrating at the approximate rate of one rotation per sec. When swimming, vibration of the anterior tip was hardly seen; it appeared quite definitely, however, when the organisms slowed down, and in particular when it suddenly changed its direction. 'On investigating these vibrations by means of the stroboscope, the maximum rate of beat was found to be 46-48 per sec., and since this somewhat regular beat or vibration can be looked upon as the rebound from each flagellum, it probably means that each flagellum was making about 24 beats per sec.' The swimming movement of this species was almost identical with that of a *Chlamydomonas* sp. examined by him. Lowndes's work (1936, 1941, 1943, 1947), on the activity of living flagella, confirmed by Brown (1945), has shown that a flagellum beats in spiral undulations with the waves of contraction progressing from the base towards the tip, the waves often increasing in amplitude as they progress. Brown also confirms Lowndes's theory that the rotation and gyration of the body alone may adequately account for the locomotion of many flagellates, without any forward component produced directly by the flagellum.

Fischer (1894), Loeffler (1889), Peterson (1918, 1929), Vlk (1938), and others, using drying and staining techniques, have described two types of



Text-figs. 24-34. ($\times 5000$.) *Isochrysis galbana* n.g., n.sp. 24-28. Young motile stage, illustrating the form variation and the variation in the shape and position of the chromatophores. 24. *c*, chromatophore; *l*, leucosin; *n*, nucleus; *o*, oil globule; *s*, stigma. 29. Fission in non-motile stage. 30. Reproduction in palmelloid phase; stage 1, spheroidal cell. 31. Reproduction in palmelloid phase; stage 1, apparent fusion of two of the spheroidal cells; nuclei could not be seen. 32. Early stage in fission of motile individual, front view. 33. Later stage in fission of motile individual, front view. 34. Separation of daughter-cells practically completed, front view.

flagellum: one which is whip-like, and one which bears fine cilia along its whole length. Brown (1945), by means of the electron microscope, investigated the structure of the flagellum of several species. He found that the flagella were of approximately uniform diameter throughout their entire length, and that each flagellum consisted of a denser axial core and a less dense sheath surrounding the core; some of the flagella also bore delicate filaments extending from the sheath. The two flagella of *Isochrysis*, studied from dried and stained preparations, are equal in length and uniform in diameter throughout their entire length; no evidence was obtained of the presence of fine cilia on either flagellum.

Two large, elongate, parietal chromatophores are present; they are usually placed laterally in the body, but their shape and position change with the change in shape of the body (Text-figs. 24-28). The chromatophores are golden-brown in colour; in actively motile individuals they appear to have a faint greenish tinge to the gold, but in older slow-moving individuals, palmelloid-phases and cysts the colour of the chromatophore lacks the slight tinge of green. A small dark red stigma, ovoid in shape, is most frequently in a median position, more rarely at the extreme anterior end. It does not project above the general surface of the cell. The nucleus, just visible in living individuals, is nearly always median; no mouth-band could be distinguished and no vacuoles are developed.

Oil and leucosin are developed as in other members of this class. Small oil drops are distributed through the general cytoplasm of the cell but the leucosin, in actively motile cells, occurs most frequently as a greyish, highly refractile, rounded mass at the extreme posterior end (Pl. I, fig. 7; Text-figs. 24, 25). In some of the smaller motile individuals from two to five small masses of leucosin may be present, and these are not always in a posterior position (Text-figs. 26, 28). The expulsion of leucosin from the body in the form of a droplet has never been observed in this species, although Carter (1937) records its occurrence in *Chromulina lunaris* Carter and *Prymnesium parvum* Carter; she concluded that the expulsion of leucosin was probably a process of excretion.

In this species the amount of leucosin present in the cells varies in different aged cultures; instead of expelling leucosin it seems to build up a large reserve. In actively dividing cultures, 2-4 weeks old, the quantity of leucosin in the cells is fairly small (Pl. I, figs. 7, 10; Text-figs. 24-28); as the cultures increase in age (over 6 weeks old), cell division is greatly reduced and the amount of leucosin in the cells increases. In still older cultures (3-4 months), the leucosin practically fills the posterior part of the cell so that the chromatophores, much reduced in size, and the nucleus, now occupy an anterior position (Pl. I, fig. 4; Text-fig. 35). The shape and size of an individual alters as the amount of leucosin increases; it becomes more pyriform, increasing very considerably in breadth and thickness, so that a cell can be 5-6 μ long, and 4-5 μ broad. These heavily laden individuals are extremely sluggish and exhibit a much

slower movement than the younger individuals. The cells packed with leucosin eventually become non-motile and either form cysts or pass into a palmelloid phase in which another form of reproduction occurs.

Asexual reproduction in this species occurs by the longitudinal division of both motile and non-motile individuals, and also by cyst formation. In the young motile stages division is most frequent in the early morning. Counts made of the numbers of individuals in both sterilized sea water and culture solution showed that individuals could divide more than once in 5 hr. When an individual is about to divide the body broadens, and division of the chromatophores occurs; one chromatophore, now divided into two, passes to each daughter-cell. A second stigma appears, frequently close to the one already present (Text-fig. 32). The two flagella of the parent pass to one daughter-cell, the other daughter-cell developing two anew; the new flagella arise frequently before the nucleus has divided but sometimes not until after separation of the two cells has already started.

Before the separation of the two daughter-cells begins the leucosin appears to break up into a number of smaller masses, some passing to each daughter-cell (Text-fig. 33). Separation of the two cells is by constriction, mainly from the posterior end (Text-fig. 34). The products of division are, nearly always, of unequal size.

In cultures more than 4 weeks old some individuals lose their flagella before division takes place (Text-fig. 29). These non-motile individuals form quite a thick layer on the bottom of a flask; their shape becomes irregular but they are not surrounded by a mucilaginous investment. Fission takes place as in the motile stage, the products of division developing flagella when the separation of the individual is almost complete or after it has been completed.

Cyst formation in *Isochrysis* takes place in 3- to 6-months-old cultures. The cysts develop inside the large pyriform individuals mentioned earlier and their development follows very closely that already described for many Chrysoomonadineae. When the large pyriform cells are about to develop into cysts they cast their flagella, but they do not form any gelatinous envelope around the protoplast; they can measure up to 8μ in length and 7μ in breadth. Each individual then secretes near the periphery a spheroidal cellulose membrane, measuring about 6μ in diameter. The membrane develops around the large posterior mass of leucosin leaving the anterior nucleus, stigma and small chromatophores external to it. It does not enclose the leucosin entirely however, since an opening remains in it; this faces the anterior end of the cell (Text-fig. 36). A great many very early cyst stages have been examined, but no evidence has been obtained to show that the opening in the membrane arises secondarily.

As the cellulose membrane of the cyst thickens and becomes impregnated with silica, the nucleus, stigma, small chromatophores and some of the cytoplasm pass into the cyst through the pore at the anterior end; a certain amount

of cytoplasm remains outside the cyst (Text-fig. 37). Once the chromatophores have passed into the cyst they become much larger in size (Text-fig. 37). The cytoplasm, external to the cyst, gradually shrinks, but it persists as a thin layer until after the anterior aperture of the cyst has been closed by a hemispherical plug measuring $1.5\ \mu$ across the base (Text-fig. 38). The plug can be seen quite clearly when pressure is exerted on an early cyst stage. The outer surface of the cyst is covered by small protuberances which can be seen quite



Text-figs. 35-40. ($\times 5000$.) *Isochrysis galbana* n.g., n.sp. 35. Older motile stage containing large mass of leucosin, front view. 36. Start of cyst formation, development of cellulose membrane round leucosin mass, front view. 37. Cyst membrane thickened, cell contents passed into cyst, front view. 38. Fully formed cyst, equatorial view. 39. Early stage in the division of the contents of the cyst, equatorial view. 40. Cyst from which contents have been liberated, plug attached to one side of the pore, equatorial view.

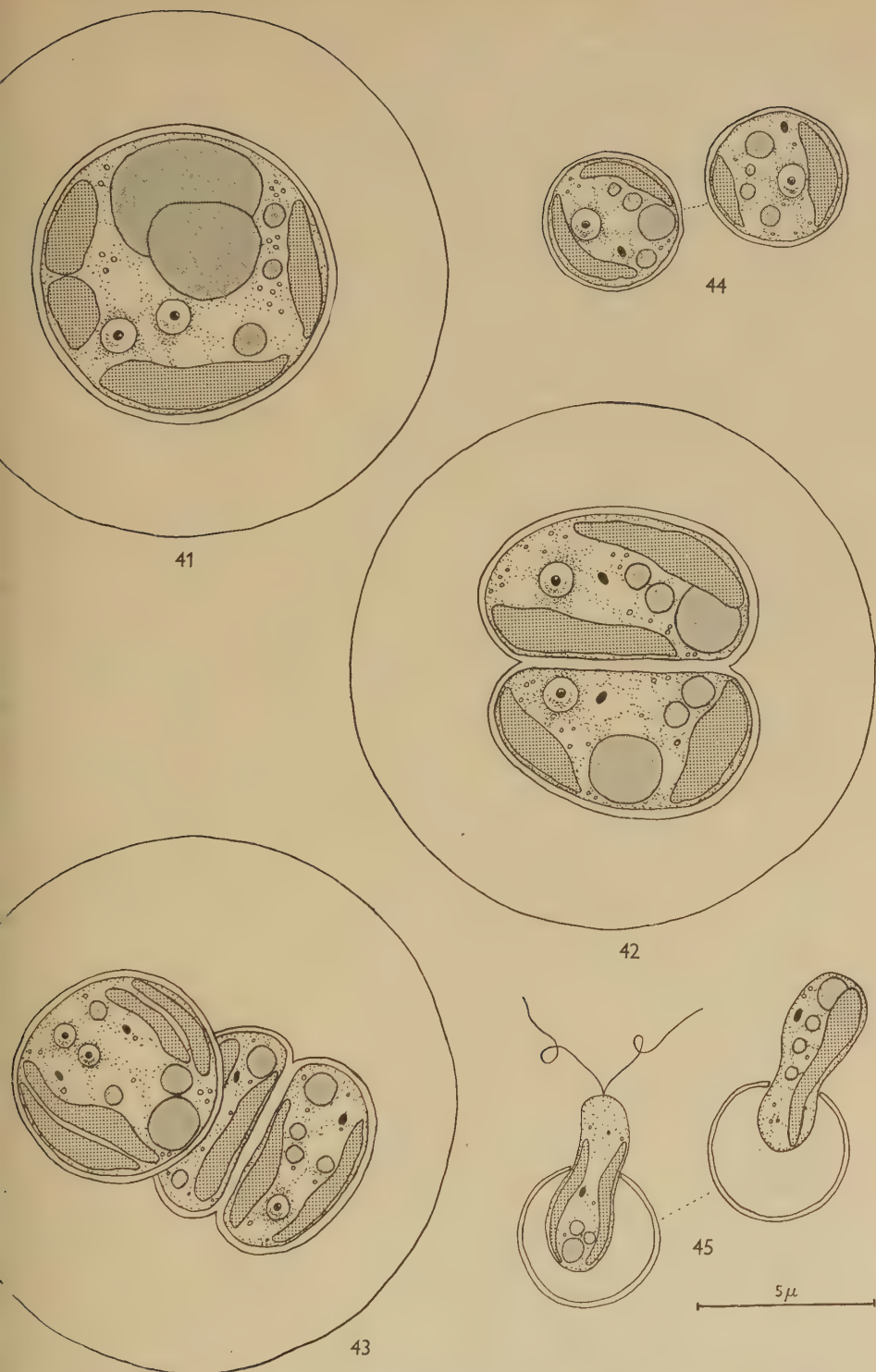
clearly after the remaining external cytoplasm has disintegrated (Pl. I, fig. 6; Text-figs. 39, 40). In this species, the spheroidal cysts, $5-6\ \mu$ in diameter, are not as large as the individuals from which they were produced; the motile individuals themselves increased in size, mainly due to the increase in the amount of leucosin present, before the production of the cysts (Text-figs. 36, 39).

In old cultures, the cyst stage can persist indefinitely without the contents showing any division. If the deposit from the bottom of an old culture (containing many cysts) is added to fresh culture solution, however, the first division stage of the contents of a cyst can be observed within 24 hr. Four divisions take place in the cyst in a line at right angles to the bottom of the

plug. Text-fig. 39 shows a cyst in which the first two divisions have been completed. In a cyst in which the contents are fully divided (Pl. I, fig. 6) sixteen naked cells are present; these cells resemble the young motile stages described earlier, possessing two chromatophores, a stigma, a nucleus and one or more small masses of leucosin. The flagella may also be developed, but they could not be seen. The cells are released from the cyst as motile individuals measuring approximately 3μ in length. The release of the individuals from the cyst does not take place by the dissolving of the plug as seems to be the usual procedure. In *Isochrysis* the plug is forced out of the pore of the cyst in an explosive manner and often remains attached to the cyst at one side of the pore (Text-fig. 40). The circular pore through which the contents escape can be seen quite clearly in the empty cyst (Text-fig. 40).

In the section on *Chromulina pleiades* reference was made to a form of reproduction in a palmelloid phase which seems to differ from any form that has been described so far for the Chrysomonadineae. Stages in this form of reproduction have been found in the four species studied, *C. pleiades* (Text-figs. 20-23), *Isochrysis galbana* (Pl. I, figs. 8, 9; Text-figs. 41-45), *Dicrateria inornata* (Text-figs. 55-60) and *D. gilva*. Although the nuclear behaviour in the early stages has not yet been elucidated, a brief description of the process, as far as is known, is given here so that similar stages in other members of the class may be recognized. It has been followed most fully in *Isochrysis*, and is therefore described under this genus.

This form of reproduction occurs in cultures which have been left at least 2 months without subculturing. The very early stages in the cycle are still not established with certainty, but there is some evidence that fusion of non-motile(?), spheroidal individuals, about 5μ in diameter, derived from the large motile, leucosin-filled individuals, starts the process (Text-fig. 30). Possible fusion stages of these cells have been seen (Text-fig. 31). The next or second stage is a larger spheroidal individual, measuring $8-9\mu$ in diameter; it is covered by a thin gelatinous envelope of firm consistency and it possesses two nuclei, two stigmata, four chromatophores and a number of large masses of leucosin (Pl. I, fig. 8). Stage 2 may be the product of the fusion of the large motile individuals which either cast or withdraw their flagella as soon as fusion starts; the non-motile spheroidal stage 1 may be individuals which have not fused. The third stage is figured on Pl. I, fig. 9, and shows that a larger secondary gelatinous envelope, of a less firm consistency than the first, has now developed; it measures about 15μ in diameter. In this stage one nucleus only is present so that the two nuclei, originally present, have either fused or one has degenerated. The third stage, therefore, may be a zygote. The fusion of motile gametes, and the subsequent reduction during the two nuclear divisions that follow the sexual fusion resulting in the formation of four daughter-cells, are recorded by Schwarz (1932) for *Ochrosphaera neapolitana* Schussnig.



ext-figs. 41-45. ($\times 5000$.) *Isochrysis galbana* n.g., n.sp. Stages in reproduction in the palmelloid phase. 41. Early stage 4, nucleus of stage 3 just divided. 42. Stage 4, first division. 43. Stage 4, second division. 44. Stage 5, products of division free from gelatinous envelope. 45. Stage 6, liberation of daughter-cells as young motile stage.

The division of the contents of the third stage may be regarded as the fourth stage. Two nuclear divisions occur (possible reduction division), the products of division remaining within the gelatinous envelope (Text-figs. 41-43). The four cells resulting from the divisions are each surrounded by a thin firm membrane of a gelatinous nature; they are spheroidal or ovoid in shape and measure not more than 4μ in diameter. The large gelatinous envelope surrounding these cells gradually disintegrates leaving the thin-walled cells free (Text-fig. 44). The contents of these cells escape from the firm envelope surrounding them as small individuals of the motile stage, measuring $3.5-4\mu$ in length (Text-fig. 45). Empty envelopes are plentiful on the bottom of a flask of an old culture and the clear circular pore, through which the contents of the cell escaped, is clearly visible. The free cells covered by the firm envelope may be called the fifth stage and the escape of the contents of the cells the sixth and last stage in the cycle.

Several stages found among the Chrysophyceae by other workers may possibly be stages in this form of reproduction. Korshikov (1929) describes, in old cultures of the colonial Chrysomonad, *Synochromonas pallida*, after the colonies had fallen into pieces, the development of solitary cells which are balled as if inflated so that their relation to the species is not readily established. He found that these cells develop a thin colourless membrane which is soft and slightly refringent. They contain large masses of leucosin, several chromatophores and two nuclei. Korshikov considers that these stages are probably early cyst stages, inside which the true cysts may eventually be formed, but says that the significance of the two nuclei is obscure. The ovoid or elliptical 'temporary' cysts in *Prymnesium parvum*, described by Carter (1937), may possibly be the end-product of the type of reproduction just described since the actual process of encystment was not observed. In these temporary cysts the membrane is thin, transparent, colourless or brownish and very delicately rugose on the exterior; the cyst lacks a plug as far as could be seen. A single individual is present in the cyst and it is released as the motile stage. Carter also records finding palmelloid groups of naked cells, two to four, in ill-defined masses of mucilage, which she believes belong to *P. parvum*.

The formation of the sporangia in *Chromulina sporangifera* given by Lund (1942) is somewhat similar in the early stages to the type of reproduction just described. In *C. sporangifera* Lund the protoplast assumes a spherical shape and increases in size, while a wide and firm mucilaginous membrane is secreted around it. The chromatophore may be divided into two or four portions, but there is no statement regarding the number of nuclei present at this stage. The later stages differ, however, since no large secondary mucilaginous envelope is developed and a great many more divisions occur so that the final product is forty or more daughter-cells instead of four.

In *C. pleiades* the first stage, the non-motile spheroidal individual (Text-fig. 20), and the second stage, the larger binucleate individual, covered

by a thin gelatinous envelope (Text-fig. 21), have been found, but neither the third stage, with the large secondary envelope, nor the fourth stage, the division of the contents of stage 3, has been seen. Although the fifth and sixth stages have been found (Text-figs. 22, 23) there is no proof at present that the large secondary envelope does develop and that two divisions only take place in *C. pleiades* during the fourth stage. The fifth stage does definitely possess, however, a very thin firm envelope from which the contents escape as motile individuals. Lund makes no reference to any thin-walled envelope around the daughter-cells from the sporangium of *C. sporangifera*; he says that when liberated they are spherical, but that they soon become actively motile and assume the ellipsoid shape.

In general form *Isochrysis* agrees rather closely with the two described species of the genus *Wyssotzкия* Lemm., but in the latter genus there appears to be considerable doubt concerning the number of flagella present; Büttner (1911, p. 126, fig. 5d, e) actually figures a third flagellum in *W. gladociliata* Lemm. Carter (1937) is of the opinion that *W. gladociliata* Lemm. is probably identical with *Prymnesium parvum* Carter and that *Wyssotzкия biciliata* (Wyss.) Lemm. belongs also to the genus *Prymnesium* and possibly also represents *P. parvum*. Conrad (1941), on the other hand, thinks that both species of *Wyssotzкия* belong to the Cryptophyceae.

Dicrateria n.gen.

Cellula natante, solitaria, nuda, periplasto differentiae carente praedita; protoplasto rigidiore, formam praebente immutabilem; cellula sphaeroidi subovata; deest sulcus; 2 flagellis, longitudine paribus, ex granulo basali distincto existentibus in parte cytoplasmatis hyalina sito; 2 chromatophoris magnis parietalibus crateriformibus fulvis contraposis; nucleo mediocri propositus polum illum sito ex quo existunt flagella; cellula pabulum holophytica; nec oleo nec leucosino indigente; sine sexu propagatur fissione per gradum mobile; cysto intra cellulam confecto; cystis sphaeroidibus subovatisque membrana externa laevi; non deest multiplicationis genus palmelloidem per gradum effectae.

D. inornata n.sp. (Flagellate 'B', Gross.)

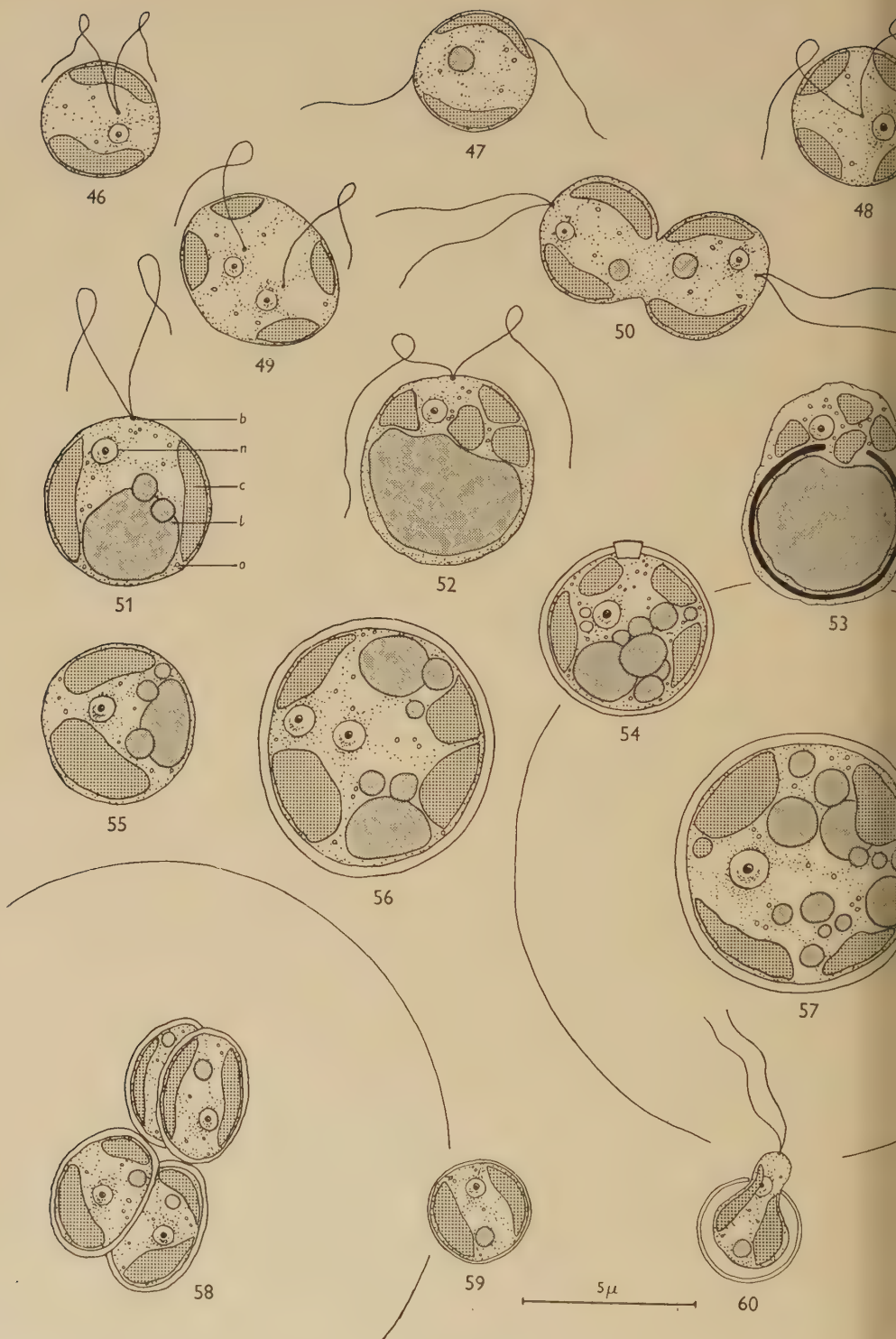
Pl. I, fig. 1; Text-figs. 46-60.)

With the characters of the genus.

Diameter of motile cells, 3-5.5 μ ; diameter of cyst, 4-5 μ .

Isolated by Dr F. Gross from an ordinary 'outside' plankton sample which was taken off Plymouth in November 1935.

The motile stage is spheroidal to slightly ovoid, and possesses a rather rigid undifferentiated periplast, which does not admit of any change of shape. In the young motile stage, two large saucer-shaped chromatophores, golden-brown in colour, are normally present; they are parietal and opposite in



Text-figs. 46-60.

position so that a clear zone of cytoplasm lies between them (Pl. I, fig. 1; Text-fig. 51). In the older motile stage four chromatophores are more frequently developed (Text-figs. 48, 52). The medium-sized nucleus is situated near to the pole from which the flagella arise and in the young stage a rather small mass of leucosin is present at the opposite pole (Pl. I, fig. 1). Small oil drops are distributed through the general cytoplasm, but the species lacks both stigmata and vacuoles.

Two equal flagella, one and a half to twice the diameter of the cell in length, arise from a distinct basal granule, or from two placed very close together, situated in the clear part of the cytoplasm (Text-figs 46, 48); they are very delicate, but can just be seen in the living cells. Stained preparations show that both flagella taper very slightly towards the free end, and neither are apparently plumate in structure. When in motion the cells rotate in a slow and steady manner and are constant in direction for relatively long periods. When swimming the flagella lie backwards down the sides of the body and carry out an undulating movement, but when at rest, they lie away from the body. Before the swimming individuals come to rest, however, they exhibit, for a short time, a peculiar dithering movement; they then remain motionless for a fairly long period. This species is slightly phototactic in reaction.

In this organism, as in *Isochrysis*, the quantity of leucosin in the cell varies in cultures of different ages (Pl. I, fig. 1; Text-figs. 51, 52). In the young actively dividing individuals, 3-4 μ in diameter, the quantity is very small (Pl. I, fig. 1), but as the culture increases in age so also does the quantity of leucosin in the cells (Text-fig. 51), until in 4- to 5-month-old cultures the leucosin may occupy from one-third to more than one-half the volume of the cell (Text-fig. 52). In the very slow-moving leucosin-filled cells, 4-5.5 μ in diameter, the chromatophores, usually four, may be so reduced in size that they appear as small disks, situated with the nucleus, at the pole from which the flagella arise (Text-fig. 52). These cells either form endogenous cysts or pass into the first stage of the reproductive cycle that takes place in the palmelloid phase.

Asexual reproduction by division of the motile cells takes place in both the light and the dark. Counts show that more than two divisions can take place within 6 hr. The procedure is similar to that described in *Isochrysis*. When

Text-figs. 46-60. ($\times 5000$.) *Dicrateria inornata* n.g., n.sp. 46. Young motile stage, viewed from pole at which flagella are inserted. 47. Young motile stage, viewed from opposite pole to Fig. 46. 48. Older motile stage with four chromatophores, viewed from pole at which flagella are inserted. 49. Early division stage of motile individual. 50. Late division stage of motile individual. 51. Older motile stage with large leucosin mass, equatorial view. *b*, basal granule; *c*, chromatophore; *l*, leucosin; *n*, nucleus; *o*, oil-globule. 52. Older motile stage with four chromatophores and still larger mass of leucosin, equatorial view. 53. Contents of cell passing into cyst, membrane of cyst thickened. 54. Mature cyst. 55-60. Stages in reproduction in the palmelloid phase. 55. Stage 1. 56. Stage 2. 57. Stage 3. 58. Stage 4, second division. 59. Stage 5. 60. Stage 6.

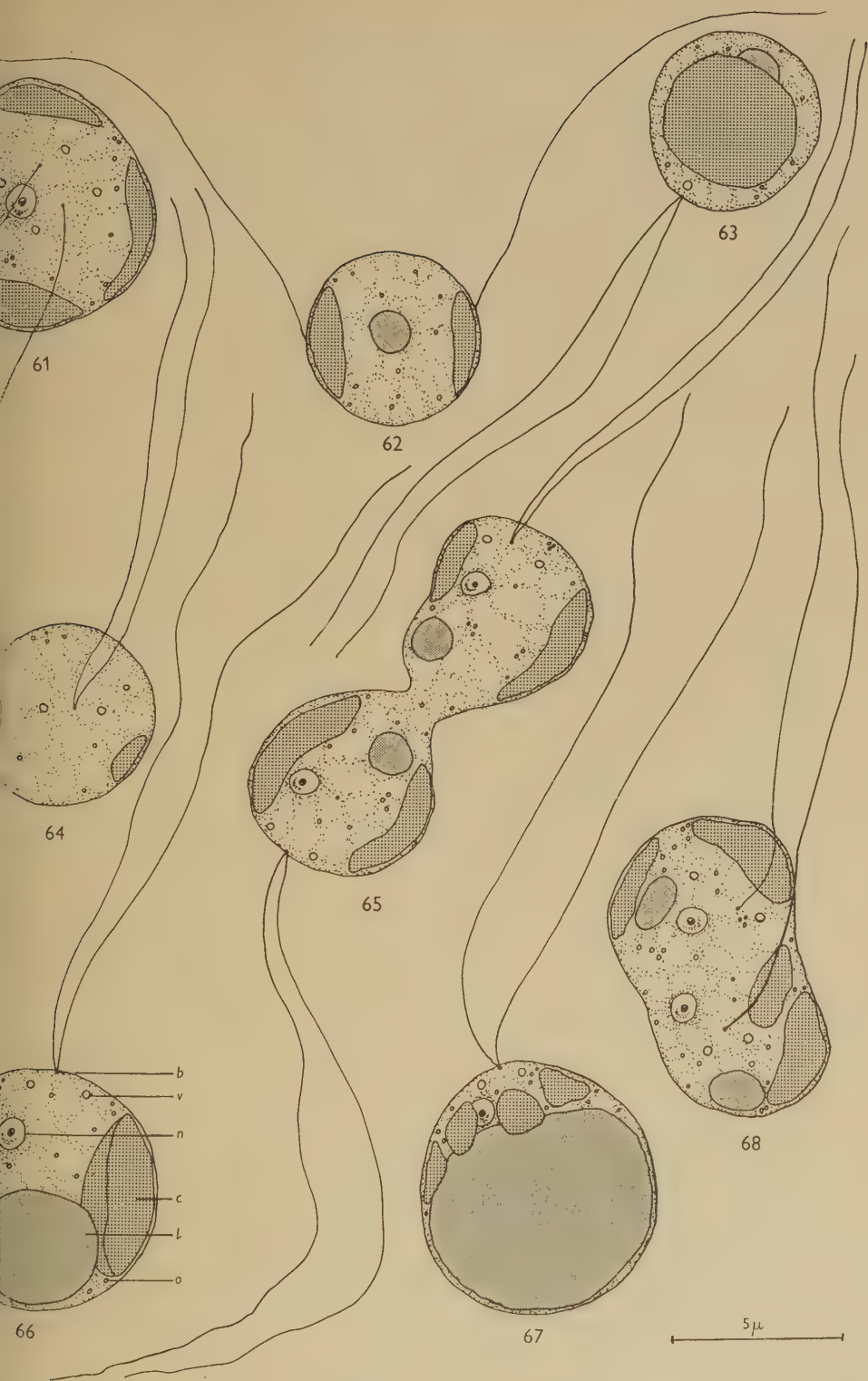
about to divide the cell broadens, the two chromatophores divide, if they have not already divided, and the leucosin breaks up into two or more smaller masses. The nucleus then divides and the two flagella separate, each attached to its basal granule or part of the basal granule (Text-fig. 49). Fission of the cell starts at the pole from which the flagella arise and passes down through the individual until the two cells are connected only at the pole away from the flagella (Text-fig. 50). A second flagellum is developed by each daughter-cell before they finally separate; the cells are usually of equal size. No loss or withdrawal of the flagella before fission has been observed in this species.

Cyst formation occurs in cultures left 5 months without subculturing. The cysts develop inside the leucosin-filled cells (Text-fig. 53) in a manner similar to that described for *Isochrysis*. The mature cysts are spheroidal with a smooth silicified wall and a plug, the shape of a truncated cone, that is raised slightly above the general surface of the cyst (Text-fig. 54).

The form of reproduction in the palmelloid phase found in the genus *Isochrysis* occurs also in this genus. In *Dicrateria inornata* the six stages in the cycle defined earlier have been obtained from old cultures (Text-figs. 55-60). The large spheroidal, leucosin-filled cells of stage 1 measure $4.5-5\mu$ (Text-fig. 55); stages in the apparent fusion of pairs of these cells have been seen, but the actual fusion of the nuclei of the cells has not yet been observed. Stage 2, the larger binucleate cell covered by a thin gelatinous envelope, has been found frequently (Text-fig. 56); it measures $7-8\mu$ in diameter. Stage 3, the uninucleate cell (Text-fig. 57), and stage 4, the division of this cell into four daughter-cells (Text-fig. 58), are not uncommon; the large secondary gelatinous envelope surrounding these stages measures $15-17\mu$ in diameter. In stage 5 the four daughter-cells become free by the disintegration of the large gelatinous envelope: they are spheroidal and are covered by a very thin, smooth, firm wall, measuring about 3μ in diameter (Text-fig. 59). Stage 6, the liberation of the contents of these cells, has also been seen; the contents escape from a small pore as a single small individual of the motile stage, measuring approximately 3μ in diameter (Text-fig. 60).

D. inornata shows some resemblance to *Chrysidalis peritaphrena* Schiller, but it is smaller and lacks the decided groove, passing forwards and backwards from the base of the flagella, which is present in that species.

Text-figs. 61-68. ($\times 5000$.) *Dicrateria gilva* n.g., n.sp. 61. Early stage in fission of motile individual, chromatophores and vacuoles doubled, viewed from pole at which flagella are inserted. 62. Young motile stage viewed from pole opposite to that at which flagella are inserted. 63. Young motile stage, equatorial view. 64. Young motile stage, viewed from pole at which flagella are inserted. 65. Late division stage, fission of cell nearly complete. 66. Older motile stage with two chromatophores and large mass of leucosin, equatorial view. *b*, basal granule; *c*, chromatophore; *l*, leucosin; *n*, nucleus; *o*, oil-globule; *v*, vacuole. 67. Older motile stage with four chromatophores, reduced in size, and very large leucosin mass, equatorial view. 68. Division stage of motile individual, nucleus and chromatophores divided, number of vacuoles doubled.



Text-figs. 61-68.

Dicrateria gilva n.sp. (Flagellate 'C', Gross.)
(Pl. I, fig. 3; Text-figs. 61-68.)

Cellula sphaeroidi subovatave; 2 flagellis cellulae diametro 3-4 plo longioribus, ex granulo basali distincto existentibus; chromatophoris fulvis pallidis, plerumque contraposis; 2 vacuolis parvis non trepidantibus ubi inserta sunt flagella fere sitis; nucleo laterali propius polum illum sito ex quo existunt flagella; cellulae mobili est diametros 5-8 μ ; cysto diametros 7-7.5 μ .

This organism appeared in a culture of a diatom started by Dr F. Gross from a plankton sample, taken within Plymouth Sound in March 1936. It is similar in form to the previous species, but shows several points of difference. The motile stage is larger, measuring 5-8 μ in diameter, and appears to have a slightly less rigid periplast (Text-figs. 63, 66).

No stigma is developed, but two small non-contractile vacuoles, lacking in the previous species, are present near the point of origin of the flagella; the chromatophores are paler in colour and possess a faint greenish tinge (Pl. I, fig. 3; Text-figs. 62-64).

The flagella, arising from one distant basal granule (or two adjacent granules), are three to four times the cell diameter in length and are therefore much longer than in the previous species; neither flagellum shows a plumate structure as far as could be seen from stained preparations. The movement of this organism differs also from that of *D. inornata*; there are alternate periods of movement and quiescence, but when swimming it shows fairly rapid movement with frequent change of direction. The position of the flagella when the cell is both in motion and at rest is the same as in *D. inornata*, but the flagella are more rigid when at rest than in the former species. This species is also phototactic in reaction.

As in the two previous species the quantity of leucosin in the cells increases with the age of the cultures (Text-figs. 66, 67). The leucosin-filled cells, with the reduced chromatophores, tend to become rather pyriform in shape; they measure 7-8 μ in length. These cells, as in the previous species, give rise to the cysts or become the first stage in the reproductive cycle in the palmelloid phase.

Asexual reproduction is by fission of the motile individuals and takes place as in *D. inornata* (Text-figs. 61, 65, 68). Stages in the formation of the cyst can be obtained from cultures 4-5 months old. The development of the cyst, inside the leucosin-filled cells, is the same as in *Isochrysis galbana* and *Dicrateria inornata*. The mature cysts are spheroidal or very slightly ovoid with a smooth silicified wall and a conical hyaline plug which is raised slightly above the surface of the cyst; they measure 7-7.5 μ in diameter. They are similar to that figured for *D. inornata* (Text-fig. 54), but are slightly larger. The release of the contents of the cyst has not been observed, but cysts from which the majority of the individuals had been released have been seen; the cells remaining in the cyst were ovoid and measured 4 μ in length.

Five of the six stages in the palmelloid form of reproduction, described in and figured for the two previous species, have been seen in this species. The first stage, measuring $6-7\mu$ in diameter, is spheroidal and shows two vacuoles and two or four chromatophores; in stage 2, the cells, covered by a thin gelatinous envelope, have four vacuoles, two nuclei and four or eight chromatophores; they measure $9-10\mu$ in diameter. The large secondary envelope of stages 3 and 4 is not of such firm consistency as in the two previous species; it measures $18-20\mu$ in diameter. The free cells of stage 5 measure $4-5\mu$, but in stage 6, the escape of the contents of these cells, has not been observed.

CRYPTOPHYCEAE

NEPHROSELMIDACEAE

Hemiselmis n.gen.

Cellula solitaria, natante, nuda, phaseliformi, dorsiventraliter depressa; squae transverse secta formam praebet ellipsoidem; periplasto perspicuo differentiam praebente praedita; sulco bene notato a margine anteriore dorsuali trans latus laterale concavum oblique currente, in superficie ventrali evanescente plane mediana sub linea; deest gula; cellulis maioribus forma valde mutabilibus; 2 flagellis disparibus lateris concavi lateralem ad partem persistentibus plane mediana sub linea; chromatophoro singulo magno, parietali; pyrenoide singulo, amyli capsula circumsaepito, in medio plerumque posito; vacuolo contractilio singulo ubi inserta sunt flagella fere sito; ocello singulo haud conspicuo ad posteriorem partem in superficie ventrali posito; nucleo parvo mediano; cellula pabulum holophytica; cellula amyli genus praebente; sine sexu propagatur fissione obliqua secundum sulcum effecta.

H. rufescens n.sp. (Flagellate 'D', Parke.)

Pl. II, figs. 11-16; Text-figs. 69-73.)

With the characters of the genus.

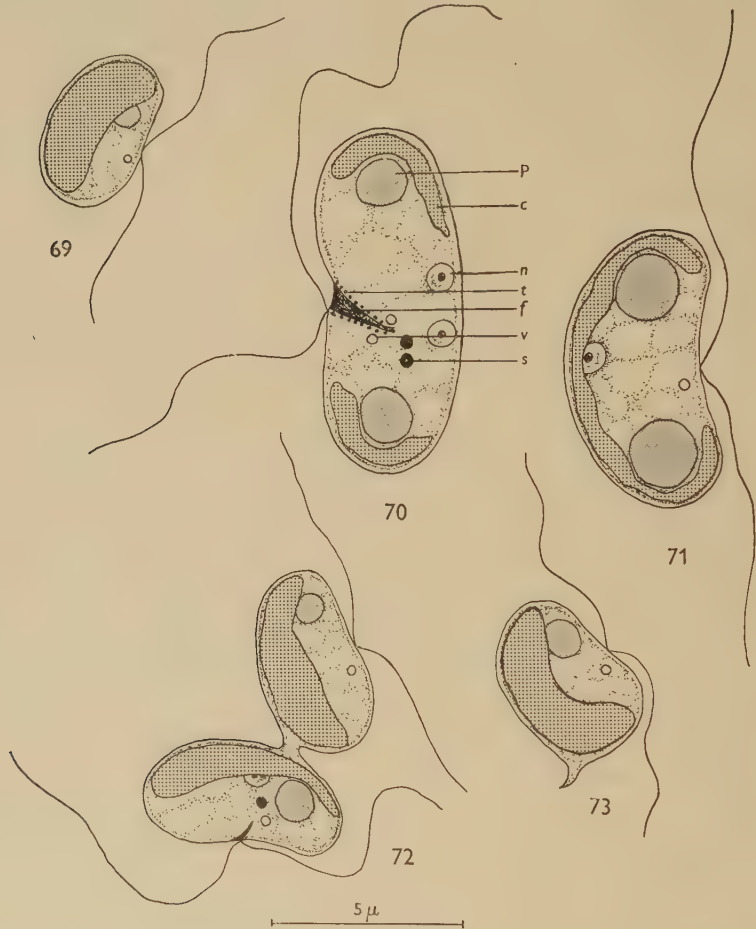
Motile cells measure $4-8.5\mu$ in length, $3.5-5\mu$ in breadth, and $2-3\mu$ in thickness.

Isolated from sea water obtained off Port Erin, Isle of Man, in April 1937.

In this species the body is bean-shaped and in the larger individuals is very flattened in a dorsiventral plane (Pl. II, figs. 11-14; Text-figs. 69, 71); in the smaller stages, however, the body is not quite so flattened. A furrow, not deepened to form a gullet, arises near the dorsal anterior edge; it runs down obliquely over the lateral edge to die out on the ventral surface just below the median line (Pl. II, figs. 12-14; Text-fig. 70).

Two delicate flagella arise laterally just below the furrow, that is, a little below the middle of the concave surface. The flagella are unequal in length,

the one directed anteriorly is about one and a half times the length of the cell and the one directed posteriorly is slightly shorter (Pl. II, figs. 11-16). No difference in the structure of the two flagella could be detected from stained preparations; neither flagellum was plumate.



Text-figs. 69-73. ($\times 5000$.) *Hemiselmis rufescens* n.g., n.sp. 69. Young motile stage, dorsal view. 70. Early division stage of motile individual, ventral view. c, chromatophore; f, furrow; n, nucleus; p, pyrenoid; s, stigma; t, trichocysts?; v, contractile vacuole. 71. Older motile individual, dorsal view. 72. Final stage in fission of motile individual, two daughter-cells just separating. 73. Daughter-cell immediately after fission has been completed, dorsal view.

The swimming of this organism has also been studied by Lowndes (1943, p. 102), and the following is his description of its movement. 'It swims rapidly, and with an enormous amount of gyration compared with the previous species (i.e. *Isochrysis galbana*). The individuals progressed in a very charac-

eristic manner traversing a spiral, the diameter of which is many times the length of the organism. It is obvious that the peculiar spiral swimming of the organism is not due to any kind of irregularity in the length or structure of the flagella, but it is dictated solely by the shape of the cell, with its strong dorsoventral flattening, and also by the fact that the flagella are attached laterally.' Movement of the cells, normally in a forward direction, is constant in direction for relatively long periods. All the cells show periods of quiescence, but these are of longer duration, and occur more frequently, in the larger individuals. This species is extremely phototactic in reaction.

The capacity to change shape is well marked in the large and in the dividing individuals, but it is not so obvious in the small stages. The periplast is clear and can be seen easily in all individuals (Pl. II, figs. 11-16). In the young stage there is a single, large, deep crimson parietal chromatophore covering about half the body surface (Pl. II, fig. 11; Text-fig. 69); it covers one lateral side and about half the surface of the ventral and dorsal sides of the body which are away from the lateral side on which the furrow arises. The edge of the chromatophore may be slightly lobed. A highly refractive, large, spheroidal pyrenoid, appearing greenish grey in colour, is present; it is normally surrounded by a sheath of solid material, which gives a blue coloration with iodine and appears therefore to be a form of starch. This organism is, therefore, undoubtedly a member of the Cryptophyceae. The pyrenoid is situated somewhat centrally in the body in most individuals and is frequently partly covered by the chromatophore (Text-fig. 69); it may be found towards either the anterior or posterior end of the body. The nucleus, round or ovoid in shape, is situated medianly or slightly posteriorly in the body, usually nearer to the ventral surface than to the dorsal. One contractile vacuole is developed immediately below the furrow in a median position in the body near the point of insertion of the flagella (Pl. II, figs. 11-13). A stigma is present on the ventral surface, placed usually near to where the furrow dies out; it can, however, be found nearer to the lateral side from which the flagella arise. In some individuals the stigma is dull in colour and difficult to detect, but its presence in this species has been confirmed for the writer by Prof. E. G. Pringsheim.

In nearly all the larger individuals two pyrenoids are present, one situated anteriorly and the other posteriorly (Pl. II, figs. 12, 14; Text-fig. 71). The quantity of starch around them has also increased so that they form large conspicuous bodies in the anterior and posterior regions of the cell. The chromatophore, now covering very little of the dorsal or ventral surface of the body (Pl. II, fig. 12; Text-fig. 71), becomes less intense in colour than in the smaller individuals, usually showing only a faint pink coloration, but occasionally becoming greenish; it may divide into two (Pl. II, fig. 14). The furrow is also more clearly defined in the large individuals. In these cells two rows of minute, highly refractive granules, probably trichocysts, can be seen, one row on either side of the furrow (Pl. II, figs. 12-14; Text-fig. 70).

Asexual reproduction in this species is by division of the cell in the motile stage (Pl. II, figs. 15, 16; Text-figs. 70, 72). Multiplication is very rapid, fission of individuals occurring in both the light and the dark. Division is oblique, the division line passing through the centre of the furrow. The large individuals, which contain two pyrenoids and two chromatophores (Pl. II, fig. 14), are probably early division stages, but the organism is more commonly found in this condition than in the small stage with one pyrenoid and one chromatophore.

When about to divide the cell becomes stretched out lengthwise, the breadth becoming slightly narrower. The nucleus then divides and a second contractile vacuole and second stigma make their appearance, usually close to the vacuole and stigma already present (Text-fig. 70). Fission starts at the anterior dorsal edge, passes down through the centre of the furrow (Pl. II, fig. 15) and continues obliquely, that is in the line of the furrow, across the cell until fission is nearly complete (Pl. II, fig. 16). The anterior chromatophore passes to the individual on the ventral side, and the posterior chromatophore to the one on the dorsal side (Pl. II, fig. 15). The two daughter-individuals, now separated except at a point below the mid-line on the convex lateral side, pull away from each other and are attached only by a very narrow connexion (Text-fig. 72). When the individuals separate, the remains of the connexion can be seen for a short while as a small papilla on the convex side of the cell (Text-fig. 73). The flagella of the dividing cell are retained by one of the daughter-cells (Pl. II, fig. 16), the other develops them anew before fission is completed (Text-fig. 72). Multiplication by fission of the motile stage is the only form of reproduction that has been found so far in this species.

This organism undoubtedly belongs to the Cryptophyceae, and adopting Pringsheim's (1944) suggested subdivision of the class, it belongs to family 5, Nephroselmidaceae Pascher, the characters of which are body bean-shaped and flagella laterally inserted. Pascher placed three genera in this family, *Nephroselmis* Stein (1878), *Protochrysis* Pascher (1911) and *Sennia* Pascher (1912), but their position in it does not yet seem to be definitely established; two species of *Nephroselmis* have been described, but the two other genera are monotypic.

Hemiselmis rufescens resembles *Nephroselmis olivacea* Stein (1878) in general shape, but appears to be more flattened. It differs from this species, however, in the absence of a gullet (as far as could be detected), in the presence of a stigma, and in the development of one contractile vacuole instead of two alternating contracting vacuoles. It is also much smaller in size and if Stein's figures (1878, Taf. XIX, figs. 36, 37) illustrate the method of fission in the motile stage of *N. olivacea*, the type of oblique fission found in *Hemiselmis* is again different. *Nephroselmis marina* Schiller (1925) is about the same size as *Hemiselmis*, but differs in shape, and lacks stigma, pyrenoid, vacuole and trichocysts. From Schiller's illustration (1925, Taf. 3, fig. 13), the flagella of

Nephroselmis marina also appear to be inserted on the convex side of the body.

Hemiselmis is very much more flattened than the genus *Protochrysis*; *Hemiselmis* differs also in its ability to change shape and in possessing a single vacuole. The lobing of the chromatophore is also very much more pronounced in the larger *Protochrysis*. A further difference is in the form of asexual reproduction; in *Hemiselmis* fission takes place in the motile stage, but in *Protochrysis phaeophycearum* Pascher it is recorded as occurring in the palmelloid phase.

The young motile stage of *Hemiselmis* is somewhat similar in shape to *Sennia commutata* Pascher, but it is more flattened. *Sennia*, however, has a fixed shape and it has only a slight indication of a furrow. The position of the nucleus in the two genera also differs.

Hemiselmis differs in colour from the three genera (golden-brown) already placed in the Nephroselmidaceae, but as Pringsheim (1944) points out, the custom of relying solely on colour as a means of generic distinction should be abandoned. There are, however, a sufficient number of differences, without the colour, to warrant the placing of this organism in a new genus.

SUMMARY

Six marine flagellates, used as food in the rearing of the larvae of *Ostrea edulis* L., are described.

One belongs to the Chlorophyceae, *Pyramimonas grossii* n.sp. (Polyblepharidaceae); four belong to the Chrysophyceae, *Chromulina pleiades* n.sp. (Chromulinaceae), *Isochrysis galbana* n.g., n.sp., *Dicrateria inornata* n.g., n.sp., *D. gilva* n.g., n.sp. (Isochrysidaceae); and one belongs to the Cryptophyceae, *Hemiselmis rufescens* n.g., n.sp. (Nephroselmidaceae).

A form of reproduction in a palmelloid phase, not previously described, is recorded for the Isochrysidaceae.

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EXPLANATION OF PLATES I AND II

PLATE I

(Figs. 1-10, $\times 7000$.)

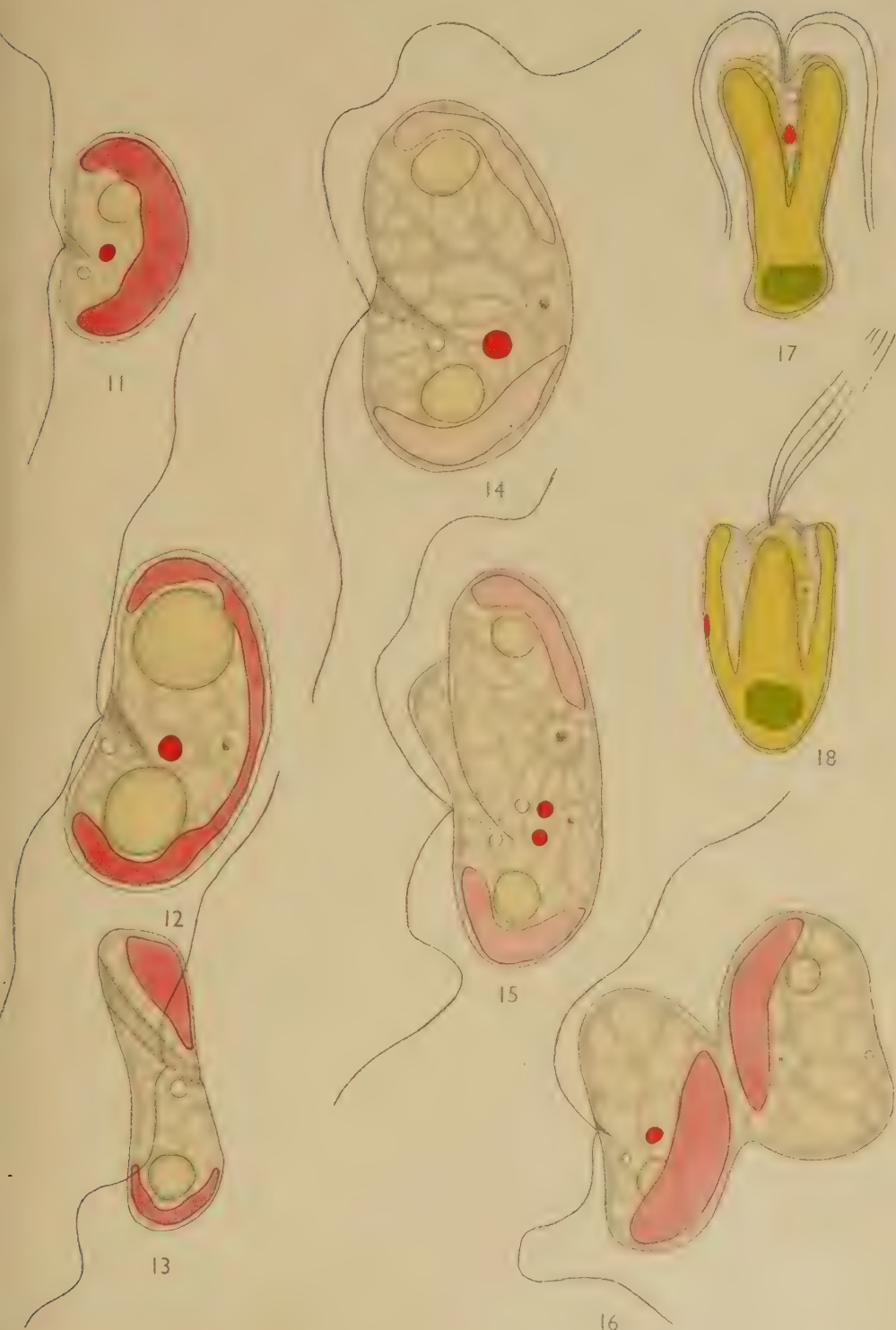
- Fig. 1. *Dicrateria inornata* n.g., n.sp., young motile stage, equatorial view.
 Fig. 2. *Chromulina pleiades* n.sp., young motile stage, from pole at which flagellum arises.
 Fig. 3. *Dicrateria gilva* n.g., n.sp., young motile stage, equatorial view.
 Figs. 4-10. *Isochrysis galbana* n.g., n.sp.
 Fig. 4. Older motile stage containing large mass of leucosin, front view.
 Fig. 5. Immature cyst, plug not yet formed, front view.
 Fig. 6. Mature cyst with division of contents completed, front view.
 Fig. 7. Young motile stage with lateral chromatophores, front view.
 Fig. 8. Reproduction in the palmelloid phase; binucleate stage 2 with narrow gelatinous envelope.
 Fig. 9. Reproduction in the palmelloid phase; uninucleate stage 3 with additional large gelatinous envelope, nucleus in early prophase.
 Fig. 10. Young motile stage, lateral view.

PLATE II

(Figs. 11-16, $\times 7000$; figs. 17, 18, $\times 4900$.)

- Figs. 11-16. *Hemiselmis rufescens* n.g., n.sp.
 Fig. 11. Young motile stage with vacuole, stigma and pyrenoid, ventral view.
 Fig. 12. Older motile stage with two pyrenoids, ventral view.
 Fig. 13. Older motile stage, lateral view.
 Fig. 14. Older motile stage with two chromatophores, ventral view.
 Fig. 15. Early division stage in motile individual showing the oblique line of fission, ventral view.
 Fig. 16. Later division stage with fission nearly completed.
 Figs. 17, 18. *Pyramimonas grossii* n.sp.
 Fig. 17. Young motile stage, showing the position of the flagella when the organism is swimming, side view.
 Fig. 18. Young motile stage, showing the position of the flagella when the organism is quiescent, side view.





THE POST-LARVAL SAND EELS (AMMODYTIDAE) OF THE CELTIC SEA AND PLYMOUTH AREA

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(Plates I & II and Text-figs. 1-6)

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INTRODUCTION

The young stages of certain species of sand-eels (Ammodytidae) can be distinguished by differences in their pigmentation. Ford (1920) has described the post-larvae of *Ammodytes lanceolatus* Lesauvage and *A. tobianus* L. The post-larva of *A. marinus** Raitt has been identified by Kändler (1941), and Page (1918) has given an account of the post-larva of *Gymnammodytes cicerellus* Rafinesque). In addition to post-larvae of *lanceolatus*, *tobianus* and *marinus*, a fourth *Ammodytes* post-larva, with a pigmentation pattern distinct from those of the above four species, has been found in collections from the Celtic Sea and Plymouth area.

The occurrence of four *Ammodytes* post-larvae in this area is of particular interest in relation to the observations of Kändler (1941), who also found four *Ammodytes* post-larvae in the southern North Sea and Baltic. He records post-larvae of *lanceolatus*, *marinus* and two forms of *tobianus*, a spring brood form and an autumn brood form, both differently pigmented. These Kändler refers to two races of *tobianus* which he is able to distinguish in the

Duncker & Mohr (1939) do not accept *A. marinus* as a separate species. The identification of the post-larva by Kändler (1941) and the specific scale distribution pattern in the adult (paper in manuscript, P.G.C.) leave no doubt, however, that it is a valid species, distinct from *A. tobianus*.

adults—the spring spawners and the autumn spawners. The pigmentation of the fourth *Ammodytes* post-larva from Plymouth and the Celtic Sea agrees very closely with the description of the pigmentation of the autumn-brood *tobianus* post-larva from the North Sea and Baltic (Kändler, 1941, p. 66).

The fourth post-larva from the Celtic Sea and Plymouth area is also of interest in relation to the four species of adult Ammodytidae (*A. lanceolatus*, *A. tobianus*, *A. marinus* and *G. semisquamatus* (Jourdain)) recorded by Raitt (1934, 1935) in Scottish waters. In this connexion, it is to be noted that Duncker & Mohr (1935, 1939), in their revision of the Ammodytidae, placed the smooth sand eels in a new genus, *Gymnammodytes*, and divided the former single European species, *A. cicerellus*, into two species, *G. cicerellus* and *G. semisquamatus*. It may be anticipated from this division that specific differences will be evident in the young stages of these two species, including differences of pigmentation which would distinguish the post-larvae of *G. cicerellus* from those of *G. semisquamatus*. The young stages of *G. cicerellus* described by Fage (1918) were all taken in the Mediterranean, with the exception of four specimens caught off the mouth of the River Tagus, Portugal. No other occurrence of a similar post-larvae is recorded throughout the widespread and detailed investigations on the young fish of European Atlantic waters. Duncker & Mohr (1939) assign all former records of *A. cicerellus* from the Mediterranean, including the post-larvae described by Fage, to *G. cicerellus*, and those from the Atlantic coastline of Europe to *G. semisquamatus**. On the basis of this distribution, the young stages of *G. semisquamatus*, if separable by differences of pigmentation according to the above inference, have not hitherto been captured or identified.

There seemed then at the outset to be two possible interpretations of the fourth *Ammodytes* post-larva from the Celtic Sea and Plymouth area. It might belong to the Atlantic *G. semisquamatus* which is known from Raitt's records of the adult to be abundant in the north-east Atlantic. Or, to judge from its close resemblance to Kändler's autumn brood *tobianus* post-larva, it might belong to *Ammodytes tobianus*. In this latter event there would then be two forms in the south-western area as well as in the North Sea and Baltic.

The present study leads, however, to the conclusion that neither of these two possible interpretations applies, and that the fourth post-larva from the Celtic Sea and Plymouth area, although undoubtedly belonging to the family Ammodytidae, is not attributable to a known species.

Before discussing the evidence which leads to this conclusion, it will be relevant briefly to review some of the previous literature.

* A strict interpretation of this would ascribe the four post-larvae caught off the mouth of the Tagus to *G. semisquamatus*. Fage, however, considered them to belong to the series of young stages of *G. cicerellus* taken in the Mediterranean. But it must be recalled that this was before Duncker & Mohr's separation of the two species.

PREVIOUS EUROPEAN RECORDS OF AMMODYTIDAE

In addition to the two commonly known British species, *Ammodytes lanceolatus* and *A. tobianus*, Raitt (1934, 1935) recorded *Gymnammodytes semisquamatus* and a new species, *A. marinus*. He found *marinus* to the north and west of Scotland and in the North Sea in greater abundance than any of the other three species. It is now also known to occur in the Irish Sea off the Isle of Man*, in addition to the present records of the young stages from the Celtic Sea and off Plymouth. Adult *marinus* have not, however, been taken in the south-eastern area. Raitt also found *G. semisquamatus* in very considerable numbers to the north and west of Scotland, but less commonly on the east coast and in the open North Sea. Before this discovery of the abundance of this species in Scottish waters, it was considered to be restricted, with the exception of a very few isolated records from northern waters (Shetlands, one specimen of *A. siculus*, Günther, 1867: Southern Norway, five specimens as *A. cicerellus*, Collett, 1904; Grieg, 1912: Sweden, Lönnberg, 1915), to the St Malo region in the southern half of the mouth of the English Channel (Jourdain, 1879; Moreau, 1891), the Atlantic coastline of France (Acloque, 1900), Portugal and Spain (de Buen, 1935). It has recently been found in the Irish Sea* and in the English Channel off Plymouth*. It did not occur in the extensive collections made by Kändler (1941) in the Baltic and southern North Sea although it is recorded by Poll (1947) from the latter area. The distribution of the adults of the European Ammodytidae may be summarized from the above records and those of other authors:

A. lanceolatus. Iceland^{1,2},† Norway³, Faroes^{1,2}, Baltic⁴, North Sea^{4,5,6}, west coast of Ireland⁶, Irish Sea⁷, English Channel⁶, France (Biscay)⁸, Spain (Biscay)⁹, Portugal (south to mouth of River Tagus)¹⁰; very rarely found in Mediterranean⁶, not recorded from Spanish Mediterranean coast⁹.

A. marinus. Greenland^{1,2}, Iceland^{1,2}, Norway¹¹, Faroes^{1,2}, Baltic⁴, North Sea^{4,5}, Irish Sea¹²; not recorded from west coast of France, Spain, Portugal, or from Mediterranean.

The present distribution records of *marinus* post-larvae have a southern limit in the mouth of the English Channel (pp. 307-9), and consequently the possibility of the species occurring even farther to the south cannot be excluded.

A. tobianus. Greenland (one specimen)¹, Iceland^{1,2}, Norway¹¹, Faroes^{1,2}, Baltic⁴, North Sea^{2,4,5}, Irish Sea⁶ (*marinus* not then distinguished), English Channel⁶ (*marinus* not then distinguished), France (Biscay)⁸, Spain⁹, Portugal⁹, Mediterranean (Balearic Islands and Spanish coast from Franco-Spanish border to Cape Nao)⁹.

The records of *tobianus* to the south of the English Channel are included here since *marinus* has not yet been identified to the south of the Channel.

* Records to be published in a further communication.

† For explanation of figures see page 291.

Day (1880-84) records *tobianus* as common round the Irish coast. The preponderance of *marinus* to *tobianus* on the west coast of Scotland (Raitt, 1934) strongly suggests that *marinus* may occur on the Atlantic coast of Ireland.

G. semisquamatus. Norway^{13, 14}, Sweden¹⁵, North Sea^{5, 16}, Irish Sea¹², western English Channel^{12, 17, 18}, France (Brittany)¹⁹, Spain (not coast of Galicia)⁹, Portugal⁹.

G. cicerellus. Mediterranean²⁰, Black Sea²⁰.

The distribution of the young stages of the European Ammodytidae cannot be so fully outlined as that of the adults owing to the fact that *tobianus* and *marinus* were not distinguished in the earlier accounts* before Kändler's (1941) identification of the post-larva of *marinus*. Only those records, therefore, in which the possibility of confusion of these two species does not occur, are included in the following summary:

A. lanceolatus. Baltic⁴, north and west coasts of Scotland¹², North Sea^{4, 12}, Irish Sea²¹, Celtic Sea²², Plymouth^{22, 23}.

A. marinus. Faroes¹², Baltic⁴, north and west coasts of Scotland¹², North Sea^{12, 20}, Celtic Sea²², Plymouth^{22, 23}.

A. tobianus. Baltic⁴, north coast of Scotland¹², North Sea^{12, 20}, Celtic Sea²², Plymouth^{22, 23}.

G. semisquamatus. Norway, Bergen (3 specimens, 47.5, 60.0 and 78.0 mm.)¹³; Channel Islands (2 specimens, 50.0 and 55.0 mm.)†; ? this species, Portugal, off River Tagus (4 specimens, 35.0-45.0 mm.)²⁴. Fage (1918) refers these specimens to the series of post-larvae of *G. cicerellus* from the Mediterranean although, as previously pointed out (p. 288, footnote), the locality of capture suggests, according to the distribution of the two species given by Duncker & Mohr (1939), that they may be attributable to *G. semisquamatus*. This possibility is given support by the fact that a detailed comparison of the distribution of the individual melanophores which make up the gross pigmentation and of the gross pigmentation itself showed no differences between the specimens of *semisquamatus* found in the Channel Islands and examples of *cicerellus* of similar size from Sebastopol in the Black Sea (12 specimens, 47.0-63.0 mm.) and also from the Naples area (21 specimens, 52.0-68.0 mm.)‡. There was, however, no difficulty in identifying the two species by their respective long (*cicerellus*) and short (*semisquamatus*) ventro-lateral skin fold (Duncker & Mohr, 1939), and all

* See Appendix on pages 311-12.

† The writers are much indebted to Miss Ursula M. Grigg for the two specimens from the Channel Islands, which, as far as is known, are the only records of any young stages of *G. semisquamatus* from British waters. They were both found dead on the sand near low water (50 mm., Petit Port, Guernsey, 7 September 1948; 55 mm., Beau Port, Jersey, 31 August 1948).

‡ The writers' thanks are due to Dr E. Trevawas, British Museum (Natural History), for permission to examine the Black Sea specimens, and to Dr R. Dohrn, Director of the Stazione Zoologica, for kindly providing the specimens from the Naples area.

these juvenile specimens were referable to the genus *Gymnammodytes* by the characteristic structure of the lateral line (Jourdain, 1879; Duncker & Mohr, 1939). Concerning the four specimens taken off the mouth of the River Tagus, Fage wrote "Il est donc impossible de distinguer ces individus de ceux à peine plus âgés (3 specimens, 10-12 cm.) pris le 21 Février 1911 à Messine...". And of the Mediterranean post-larvae of *G. cicerellus*, he observed that the striking melanophore pattern of the earlier stages (Figs. 5 & 6; 7.5 and 11.0 mm.; Fage, 1918) becomes less pronounced with increased size (Fig. 7; 25.0 mm.; Fage, 1918). There is thus, in the late post-larvae and juveniles of these two species of *Gymnammodytes*, a similar difficulty of specific identification (by pigmentation alone) to that found in the same stages of the three species of *Ammodytes* (p. 294), although no such difficulty occurs in the earlier stages of the *Ammodytes* spp.

G. cicerellus. Western Mediterranean, Alboran Sea, Balearic Islands, Tyrrhenian Sea, Straits of Messina²⁴; eastern Mediterranean, off Alexandria²²; ? this species, Portugal, off River Tagus²⁴ (see above).

¹ Bruun (1941).

² Jensen (1941).

³ Wollebæk (1924).

⁴ Kändler (1941).

⁵ Raitt (1934).

⁶ Day (1880-84).

⁷ Moore (1937).

⁸ Joubin & LeDanois (1924).

⁹ de Buen (1935).

¹⁰ Gonçalves (1942).

¹¹ Soleim (1945).

¹² Records to be published in a further communication.

¹³ Collett (1904).

¹⁴ Grieg (1912).

¹⁵ Lönnberg (1915).

¹⁶ Poll (1947).

¹⁷ Jourdain (1879).

¹⁸ Moreau (1891).

¹⁹ Acloque (1900).

²⁰ Duncker & Mohr (1939).

²¹ Bal (1944).

²² Present records.

²³ Ford (1920).

²⁴ Fage (1918).

PROBLEMS IN IDENTIFYING THE POST-LARVAE

The pigmentation of the *A. lanceolatus* and *A. tobianus* post-larvae in the present collections is in full agreement with the figures and descriptions given by Ford (1920), and the pigmentation of the *A. marinus* post-larvae agrees with Kändler's (1941) figure and description. The pigmentation of the post-larva of *G. cicerellus* (Fage, 1918, Figs. 5-7) is strikingly different from that of the above three species and from that of the species IV post-larva occurring in the Celtic Sea and Plymouth area. It has already been mentioned that the two post-larval forms of *tobianus* from the southern North Sea and Baltic are each distinguishable by a different pigmentation pattern (Kändler, 1941). The post-larvae of the spring brood (*id.*, fig. 3c, p. 64) are more heavily pigmented in general than those of the autumn brood (*id.*, p. 66), and Kändler (*id.*, p. 65) identifies the darker spring form with the Plymouth *tobianus* post-larva described by Ford (1920). Ford's specimens were caught in late summer, July, August and September (Clark, 1920), and the *tobianus* post-larvae of the present collections also show a maximal occurrence in August and September (Table III, p. 304).

As earlier remarked, the melanophore pattern of Kändler's more lightly pigmented autumn brood *tobianus* post-larva, of which he gives a full description, but unfortunately no figure, very closely resembles the pigmentation of the species IV post-larva which occurs in this area in the spring (Table III, p. 304).

It is important to emphasize the agreement of pigmentation in the lightly pigmented pair of post-larvae (species IV, this area; *tobianus*, North Sea and Baltic, Kändler) and in the dark pair (*tobianus*, this area, Ford; *tobianus*, North Sea and Baltic, Kändler), since the times of occurrence of each member of the two pairs are exactly opposite in the two areas:

	Celtic Sea and Plymouth		Southern North Sea and Baltic	
	Light form	Dark form	Light form	Dark form
Spring	Species IV	<i>tobianus</i> (Ford)	<i>tobianus</i> (Kändler)	<i>tobianus</i> (Kändler)
Autumn	..	..	..	..

Notwithstanding this inversion in the times of occurrence, the two forms from each of the two areas might well be considered on the criterion of pigmentation to be identical. If this were so, a spring brood and an autumn brood of *tobianus* post-larvae, similar to the double brood found by Kändler in the North Sea and Baltic, could be recorded from Plymouth and the Celtic Sea. This appears, however, to be excluded by the following evidence obtained from a study of the number of vertebrae in the post-larvae (Table II and pp. 301-4).

There is a separation of 5.67 ± 0.400 between the means of the number of vertebrae of the *tobianus* (66.33 ± 0.360) and species IV (72.0 ± 0.175) post-larvae from Plymouth and the Celtic Sea, and there is no overlap in their ranges (*tobianus*, 64-69: species IV, 70-74). A difference of this magnitude between the mean vertebral numbers of the two different *Ammodytes* post-larvae occurring in the same area, although at different seasons, is considered to preclude the possibility of their belonging to the same species.

Although Kändler has not examined the number of vertebrae in the post-larval *tobianus* of the spring and autumn broods from the southern North Sea and Baltic, his counts of adult spring and autumn spawners show only a very small difference of less than 1.0 between their means (Kändler, 1941, Table 25, p. 122):

	North Sea	Baltic
Spring	63.09	63.17
Autumn	64.08	63.49
Difference	0.99	0.32
Error of difference	± 0.071	± 0.061

It is noteworthy that the means of the North Sea and Baltic autumn-spawning adult *tobianus* (64.08 North Sea; 63.49 Baltic), which give rise to the autumn brood of post-larvae with the light pigmentation corresponding to species IV, are considerably lower than the mean of the *tobianus* post-larvae

(66.33) from this area. The differences (7.92, 8.51) between the means of these North Sea and Baltic autumn-spawning adult *tobianus* and that of species IV are thus even greater than the difference (5.67) between the means of species IV and the *tobianus* post-larva of this area. It is considered as before that these wide differences preclude the possibility of identifying the species IV post-larva with the *tobianus* post-larvae, in particular the light form, from the North Sea and Baltic.*

It has already been mentioned that the pigmentation of the post-larvae of *G. cicerellus* described by Fage (1918) is very distinct from that of the species IV post-larvae, and also that no post-larvae have hitherto been found which can be attributed to the adult *G. semisquamatus*, which occurs commonly in Scottish waters (Raitt, 1934). A sample of these Scottish *G. semisquamatus*† was found to have a mean vertebral number of 68.16 ± 0.127 (Table II, p. 302). This figure is 3.84 ± 0.022 less than the mean of species IV (72.0), and although it is the nearest approach to the species IV mean, it seems highly unlikely that an adult with a mean vertebral count of 68.16 could be related to a post-larva with a mean of 72.0, even allowing for geographical variation.‡

It is therefore concluded from the above evidence that the post-larval *Ammodytes* species IV is not related to the Atlantic *Gymnammodytes semisquamatus* or to *A. tobianus* from either the Celtic Sea and Plymouth area or the southern North Sea and Baltic.

It appears then that the species IV post-larva cannot be attributed to a known adult, and it can only be concluded that it belongs to another species of *Ammodytes*. If this interpretation proves to be correct, the number of species of Ammodytidae in the Celtic Sea and Plymouth area is thus increased to five:

Adult:	<i>A. lanceolatus</i>	<i>A. tobianus</i>	<i>G. semisquamatus</i>	Not recorded	Not known
Post-larva:	<i>A. lanceolatus</i>	<i>A. tobianus</i>	Not recorded	<i>A. marinus</i>	Species IV

The description (pp. 299–500) and figures (Pl. II, fig. 2) of the species IV post-larva show that the type of development, the general body form and the scheme of pigmentation all very closely resemble the same characters in the post-larvae of *lanceolatus*, *tobianus* and *marinus*, and such conformity is held to substantiate the inclusion of species IV in the family Ammodytidae, although no certain distinction between the genera *Ammodytes* and *Gymnammodytes* can be made.

No great numbers of adult Ammodytidae have been collected and examined from this south-western area. With sufficient search it appears likely that adult

* Kändler's vertebral counts of adult *tobianus* from the North Sea and Baltic are here taken as representative of the vertebral counts of the post-larvae from the area.

† These specimens, part of Dr D. S. Raitt's original material, were kindly provided by Dr R. S. Clark, lately Director of the Marine Laboratory of the Scottish Home Department, Aberdeen.

‡ There are no vertebral count data of Mediterranean *G. cicerellus* from which a mean can be calculated. Fage (1918) gives the range as 66–69 and Duncker & Mohr (1939) give the figure 67 (39+28). It is not stated whether these figures are inclusive or exclusive of the urostyle.

marinus will be found. It remains to be seen whether further search will also bring to light the adult of species IV.

Despite the almost exclusive relation to post-larval stages of the present data, it is felt that they are worth publication in order that the numerous questions which call for further study may be brought to the notice of other workers. Some of the questions awaiting solution are at once apparent.

Vertebral count data of adult *lanceolatus*, *marinus* and species IV from this area are needed for comparison with the present post-larval data.

Further data are required to resolve the anomalous difference between the number of vertebrae in adult and post-larval *tobianus* from this area (p. 303).

A search for the adult of species IV must be made and, if successful, its identification will need to be established.

These problems arise directly from the present study. Others of wider relevance are also evident. Thus vertebral count data of both adult and post-larval *G. cicerellus* from the Mediterranean are required; while intimately connected with this is the need for continued search for the post-larva of the Atlantic *G. semisquamatus*, and for an investigation of the breeding habits of this species.

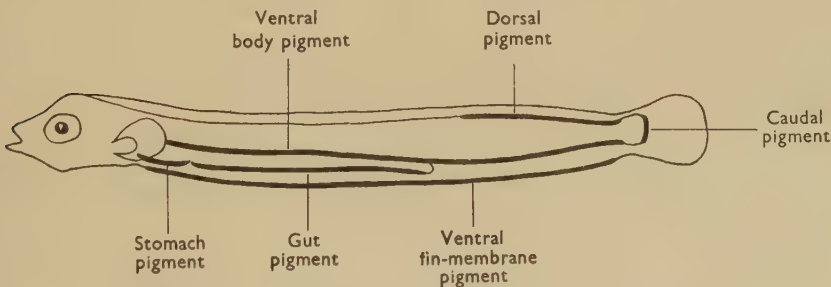
Of rather different character, but none the less important, is the need for full confirmation of the identification of the known Ammodytidae post-larvae with the known adults. *A. lanceolatus* appears to be the only species in which the post-larvae can with certainty be linked with the adult (pp. 301-3). The available facts give every indication that the post-larvae of *A. tobianus*, *A. marinus* and the Mediterranean *G. cicerellus* are correctly assigned to their respective adults. It must, however, be admitted that the chain of evidence is not entirely complete. In none of these three species has it yet been possible fully to apply Schmidt's classic method of seriation from early larva to adult or recognizable adolescent. The frequently encountered difficulty of obtaining a full series of adolescent stages, intermediate between the late post-larva and the juvenile with adult characters, may be in part responsible for the gap. Moreover, in *lanceolatus*, *tobianus* and *marinus*, the specificity of the post-larval pigmentation lessens with increasing age until it is extremely difficult to separate the late post-larvae and early adolescents. Rearing from artificial fertilizations of known parentage should, however, provide material for comparison with the existing descriptions of the post-larvae of *A. tobianus*, *A. marinus* and *G. cicerellus*. But the difficulty of rearing a large enough number of young stages to a size suitable for alizarin staining presents considerable obstacles to the solution of the vertebral count problems. And were it achieved, it is certain that the laboratory conditions would greatly differ from the spawning ground conditions which are generally thought to have considerable influence on the definitive number of vertebrae.

MATERIAL

The material for the present paper was collected by standard $\frac{1}{2}$ hr. oblique hauls of the 2 m. stramin ring-trawl on the 1937-39 mackerel investigation cruises in the Celtic Sea (Corbin, 1947), and in the weekly plankton collections of 1930, 1931 and 1935-37 taken near the Eddystone light-house for the purpose of observing the yearly fluctuations in the abundance of young fish in the Plymouth area (Russell, 1930-47). More than 6000 *Ammodytes* post-larvae from the 1937-39 cruises have been examined together with some 850 specimens from the Plymouth collections. They range in length from about 5 mm. to about 30 mm. The writers are much indebted to Mr F. S. Russell for the loan of the Plymouth young fish collections of 1930-37 and of specimens of *G. cicerellus* post-larvae from the Eastern Mediterranean off Alexandria, and to Mr G. M. Spooner for his help with the calculations. Further acknowledgements occur in the text.

THE PIGMENTATION OF THE POST-LARVAE

The nomenclature used to describe the pigmentation of the post-larvae is shown in Fig. 1. An identification key is given on p. 300.



Text-fig. 1. Diagram showing the nomenclature of the pigment rows.

Ammodytes lanceolatus (Plate I, fig. 1)*Post-larva* 4.5 mm. (a)

The fin-membrane is entire from the head, round the body and tail to the throat. Ventral body pigment extends from behind the head to the tail; it is a double line of melanophores in the pre-anal region, a single line post-anally. The stomach pigment and gut pigment form a single row of melanophores, but are distinguishable by the closer spacing of the melanophores on the stomach. Ventral fin-membrane pigment is present as a row of melanophores extending from the stomach nearly to the tail. There is seldom any indication of a dorsal pigment row at this early stage.

Post-larva 7.5 mm. (b)

The fin-membrane is still complete. Ventral body pigment, stomach, gut and ventral fin-membrane pigment rows are as in the preceding stage. The first rudiments of caudal fin-rays show ventrally to the tip of the notochord, and caudal pigment is present as one or two melanophores at the base of the developing rays. The specimen illustrated has rather heavier caudal pigmentation than is usual at this stage. Dorsal pigment is represented by two or three melanophores in the immediate pre-caudal region. The specimen figured is in this respect also slightly more heavily pigmented than typically.

Post-larva 12.5 mm. (c)

The dorsal and ventral fin-membranes are still complete, and dorsal and anal fin-rays are developing post-anally. Caudal fin-rays are well developed. Dorsal, caudal, ventral, stomach, gut and ventral fin-membrane pigmentation is similar to the preceding stage. Post-anally the ventral body pigment is a double row of melanophores almost to the tail. Teeth-like structures (Ford, 1920) are present on the upper jaw. It is of interest to compare this figure with the specimen illustrated by Ford (1920, Fig. 1, p. 243) which, although very slightly smaller (12.0 mm.), shows considerably more development of the dorsal, caudal and anal fin-rays, and almost complete disappearance of the ventral fin-membrane and loss of its pigment line.

The ventral fin-membrane pigment row is characteristic of the earlier post-larva of *lanceolatus* only; it is not present in *marinus*, *tobianus* or species IV.

Post-larva 18.5 mm. (d)

The ventral fin-membrane has almost completely disappeared. The anal fin-rays are fully or almost fully developed. The dorsal fin-rays are further developed but are still absent pre-anally in the reduced fin-membrane. The dorsal and caudal pigment is slightly more developed. Pre-anally the ventral body pigment is very much less distinct than post-anally and is only visible by transparency through the abdominal walls. It becomes obscured by the thickening and downward growth of the walls of the abdomen. The stomach and gut pigment is much reduced at this stage or even absent. Teeth-like structures are present on the upper jaw.

Post-larva 26.5 mm. (e)

Fin-rays are developed throughout the length of the dorsal fin. The dorsal pigment extends from the tail to just in front of the anus and is considerably more developed than in the preceding stage. The caudal pigment has increased. The pre-anal ventral body pigment is further obscured. The gut pigment is lost and the stomach pigment may be absent (as in the specimen figured) or represented by one to four small melanophores, seldom more.

Ammodytes marinus (Plate I, fig. 2)*Larva* 6.25 mm. (a)

The fin-membrane is entire and an oil globule of considerable size is present. The earliest stages of *lanceolatus*, *tobianus* and species IV taken in the present collections are smaller than this larval *marinus*, but none has an oil globule. Dorsal pigment is absent. Ventral body pigment is present as a row of melanophores extending from behind the head to the end of the notochord. Pre-anally the row is double, post-anally it is single. The four or five terminal melanophores are not always as prominent as in the specimen illustrated. Stomach pigment is present. Gut pigment is lacking.

Post-larva 7.5 mm. (b)

Pigmentation is similar to the preceding stage. The oil globule has been resorbed. The first indications of the developing caudal fin-rays are present.

Post-larva 11.0 mm. (c)

The dorsal pigment row is present as two or three melanophores. Considerable development of the caudal fin-rays is evident, and what will later be the caudal pigment row is clearly seen at the base of the caudal rays. Other pigmentation resembles the preceding stage.

Post-larva 14.0 mm. (d)

Dorsal and ventral fin-rays are starting to develop in the post-anal region. The caudal pigment forms a prominent line of melanophores at the base of the caudal fin-rays which are now well developed. A slight increase in the number of melanophores in the dorsal pigment row is usual at this stage, although not apparent in the specimen figured. The gut pigment develops at this stage or a little earlier; it shows considerable variation. It may consist of a well-marked regular line of melanophores from stomach to anus, it may be completely lacking, or it may be an incomplete and interrupted row (see below, post-larvae of 18.5 and 19.0 mm.).

Post-larva 18.5 mm. (e)

The dorsal and anal fin-rays are almost fully developed in the post-anal region. Fin-ray development is not yet complete in the pre-anal region where the dorsal fin-membrane is reduced. The dorsal pigment is slightly increased and some gut pigment is present.

Post-larva 19.0 mm. (f)

This specimen which is at the same developmental stage as the above specimen of 18.5 mm., has generally heavier pigmentation, particularly in the dorsal row and on the gut.

Post-larvae 23.0 and 27.5 mm. (g and h)

A forward extension of the dorsal pigment is seen in these specimens. Other pigmentation remains essentially the same. Fin-ray development in the dorsal fin is complete.

From about 10 mm. onwards, the pre-anal ventral body pigment of *marinus* is very prominent. Although situated on the inner side of the walls of the abdomen, it remains markedly conspicuous and is not obscured by the increasing thickening of the developing abdomen wall until a much later stage than in *lanceolatus*, *tobianus* and species IV.

Ammodytes tobianus (Plate II, fig. 1)

Post-larva 5.25 mm. (a)

The fin-membrane is entire. The dorsal pigment consists of two melanophores situated a short distance forward of the tip of the notochord. The ventral body pigment extends from behind the head to a point just short of the tip of the notochord. Stomach pigment consists of a closely spaced row of melanophores which under certain conditions of expansion give the appearance of an almost continuous line. The gut pigment line continues on from the stomach pigment to the anus, but the melanophores are more openly spaced than in the stomach pigment line.

Post-larva 8.0 mm. (b)

The dorsal pigment row has developed considerably since the preceding stage. There is a small pre-anal group of melanophores and a fairly well-developed row post-anally. This interrupted appearance of the dorsal row, before the development of an unbroken line, is very characteristic of the earlier post-larvae of *tobianus*. Kändler (1941) makes this observation. Caudal fin-rays have begun to develop, but no dorsal or anal rays yet.

Post-larva 8.75 mm. (c)

Dorsal and anal fin-rays have begun to develop in the post-anal region. The caudal fin rays are well developed. The dorsal pigment line has increased since the preceding stage; it extends the full length of the body from the nape of the neck to the tail. It is more pronounced in the post-anal half; the melanophores are regularly spaced and larger than those in the pre-anal region where the spacing is somewhat uneven. The pre-anal ventral body pigment is less prominent than the post-anal section owing to the opacity of the abdomen walls. The contrast between the close spacing of the stomach pigment and the open spacing of the gut pigment is more evident here than in the earlier stage. No caudal pigment is present.

Post-larva 11.0 mm. (d)

Pigmentation is very similar to the preceding stage. Fin-ray development is further advanced.

Post-larva 15.5 mm. (e)

Fin-ray development in the dorsal fin is complete. For comparison it may be recalled that no pre-anal dorsal fin-rays are present in *lanceolatus* and *marinus* post-larvae of 18 or 19 mm. Ford (1920) observed this earlier development in *tobianus*. The dorsal pigment is complete from the neck to the tail, but is still more prominent in the posterior half. Two caudal melanophores are present. The gut pigment line is slightly broken.

Post-larva 23.0 mm. (f)

Caudal pigmentation is considerably increased. A medio-lateral line has begun to develop posteriorly. The pre-anal ventral body pigment is entirely obscured by thickening of the abdominal wall. The gut pigment line is further broken and reduced, but the stomach pigment is still prominent and characteristically closely spaced.

*Ammodytes species IV (Plate II, fig. 2)**Post-larva 5.5 mm. (a)*

The fin-membrane is entire. Dorsal pigment is represented by three melanophores in the pre-caudal region. Ventral body pigment extends from the region of the stomach to the tail, but not to the extremity of the notochord. Stomach pigment is present, but no gut pigment.

Post-larva 9.0 mm. (b)

Considerable caudal fin-ray development is evident. The dorsal pigment line now extends from the position of the anus to the root of the tail. No caudal pigment is present.

Post-larva 13.0 mm. (c)

Dorsal and anal fin-rays are beginning to develop in the post-anal region of the fin-membranes, and caudal fin-ray development is further advanced. Pigmentation is similar to that of the preceding stage. The dorsal and post-anal ventral body pigmentation is more pronounced.

Post-larva 17.5 mm. (d)

Caudal and anal fin-ray development is complete. Dorsal fin-rays are starting to develop pre-anally. A slight forward increment of the dorsal pigment is evident. A single melanophore is present at the base of the caudal fin-rays. The pre-anal ventral body pigment is becoming obscured by the thickening of the abdominal walls.

Post-larva 26.0 mm. (e)

Dorsal fin-ray development is complete. The dorsal pigment row has extended forward to the neck region, but post-anally it is more prominent.

Caudal pigmentation is now fairly pronounced. A medio-lateral pigment line is present in the pre-caudal region.

The foregoing descriptions of the pigmentation of *lanceolatus*, *tobianus*, *marinus* and species IV post-larvae have been confined to the longitudinal pigment rows shown in the diagram in Text-fig. 1. Another pigmentation feature common to *marinus*, *tobianus* and species IV, but not found in *lanceolatus*, is the presence of a melanophore at the base of each pectoral fin. This pair of pectoral melanophores is present in the post-larvae of *marinus* and species IV from a length of about 10–12 mm. onwards. In *tobianus* it is generally present earlier, from a length of about 7–8 mm.

Certain additional differences both of pigmentation and form are also to be noted. Ehrenbaum (1904) observed that the length of the upper jaw in relation to the diameter of the eye is greater in *lanceolatus* than in *tobianus*. Ford's (1920, Table II, p. 245) detailed measurements of these features show that this difference is apparent at all observed lengths but becomes particularly marked above a length of 8–10 mm. It was immediately noticeable in the mixed hauls of the present collections that the snout of the *lanceolatus* post-larvae is relatively longer than that of *marinus* and species IV as well as that of *tobianus*. Ford (1920) also noted that *tobianus* post-larvae are more advanced in structural development than *lanceolatus* post-larvae of the same length, and, it may now be added, than *marinus* and species IV post-larvae. The earlier development of the pectoral melanophores referred to above and the earlier replacement of cartilage by bone (p. 301) in *tobianus* post-larvae is in agreement with this observation. It should be further noted that the differences in the caudal pigmentation of the early and middle post-larvae of the four species described are lost in the late post-larval stage when the development of fin-rays is complete in the dorsal fin. The caudal pigment is then present in each of the four species as a row of melanophores at the base of the caudal fin-rays (Pl. I, fig. 1e, fig. 2h; Pl. II, fig. 1f, fig. 2e).

*Identification key to the Ammodytes post-larvae of the Celtic Sea
and Plymouth area*

- | | | |
|-------|---|-----------------------|
| 1 (2) | Ventral fin-membrane pigment row present. Pectoral melanophores absent. Teeth-like structures on upper jaw present. Vomerine teeth present. | A. lanceolatus |
| 2 (1) | Ventral fin-membrane pigment row absent. Pectoral melanophores present. Teeth-like structures on upper jaw absent. Vomerine teeth absent. | 3 |
| 3 (4) | Caudal pigment strongly marked from earliest post-larval stage; not always present in earliest larvae with large oil-globule. | A. marinus |
| 4 (3) | Caudal pigment absent or very reduced until late post-larval stages. | 5 |
| 5 (6) | Ventral gut pigment present. | A. tobianus |
| 6 (5) | Ventral gut pigment absent. | A. species IV |

THE NUMBER OF VERTEBRAE IN THE POST-LARVAE AND ADULTS

The number of vertebrae was counted in alizarin-stained post-larvae of *lanceolatus*, *marinus*, *tobianus* and species IV. These data are given in Table I, together with a count of the number of vertebrae in a sample of adult *tobianus* from Exmouth (September 1947)*. Counts were made only from those specimens in which staining revealed that bone had fully replaced cartilage. This takes place in *tobianus* post-larvae at a length of about 13 mm., whereas *lanceolatus*, *marinus* and species IV post-larvae will not successfully stain below a length of 18–19 mm. This difference is in agreement with the previously noted earlier development of *tobianus* post-larvae.

TABLE I. THE NUMBER OF VERTEBRAE IN THE POST-LARVAL *AMMODYTES* SPP. OF THE CELTIC SEA AND PLYMOUTH AREA

Number of specimens

No. of vertebrae (including urostyle)	<i>A. tobianus</i>					<i>Ammodytes</i> species IV (post-larvae)
	Post-larvae	Adults (Exmouth)	<i>A. lanceolatus</i> (post-larvae)	<i>A. marinus</i> (post-larvae)		
62	..	1	..	..		..
63	..	12	..	..		..
64	1	23	1	..		..
65	1	10	..	..		..
66	6	6	1	..		..
67	2	..	9	5		..
68	1	..	24	16		..
69	1	..	15	18		..
70	..	..	2	6		2
71	..	..	..	..		4
72	..	..	..	..		16
73	..	..	..	..		4
74	..	..	..	..		2
Total no. of specimens	12	52	52	45		28
Mean verte- bral no.	66.33	64.15	68.08	68.56		72.00
Standard error of mean	± 0.360	± 0.134	± 0.082	± 0.128		± 0.175
σ	1.247	0.969	0.997	0.857		0.926

Alizarin staining of post-larval *lanceolatus* clearly showed the denticles on the upper jaw, a specific recognition character of the post-larva (Ford, 1920), and also made visible the pair of teeth on the vomer. It is of some importance to draw attention to the vomerine teeth in the post-larva of *lanceolatus*. They are a primary specific character of the adult. But as far as is known, there is no reference in the literature to their presence in the post-larva, which thus establishes a complete chain of specific characters in the development of *lanceolatus* from the late larva to the adult. The ventral fin-membrane pigment

* The writers are indebted to Mr N. A. Holme for kindly obtaining these specimens.

TABLE II. THE NUMBER OF VERTEBRAE IN THE NORTH ATLANTIC SPECIES OF AMMODYTIDAE

The standard deviation (σ) and the standard error of the mean have been calculated from the data of the author quoted, with the exception of Kändler (1941), who gives values for the latter.

	Author	No. of specimens	Mean no. of vertebrae	Standard error of mean	Range of no. of vertebrae	σ
A. tobianus						
Iceland	Bruun (1941)	52	62.56	± 0.125	60-65	0.902
Faroes	Bruun (1941)	22	64.45	± 0.200	63-66	0.940
Baltic, spring spawners	Kändler (1941, table 25, p. 122)	961	63.17	± 0.033	60-67	1.035
autumn spawners		566	63.49	± 0.051	60-67	1.216
North Sea, spring spawners		274	63.09	± 0.057	61-65	0.944
autumn spawners		566	64.08	± 0.043	61-68	1.031
Northern North Sea	Raitt (1934)	199	63.37	± 0.063	60-66	0.984
Denmark	Jensen (1941)	82	63.37	± 0.108	61-65	0.982
Exmouth	Present records	52	64.15	± 0.134	62-66	0.969
Plymouth, post-larvae	Present records	12	66.33	± 0.360	64-69	1.247
A. lanceolatus						
Baltic	Kändler (1941, table 23, p. 120)	126	66.73	± 0.076	65-69	0.853
North Sea		293	66.85	± 0.047	65-69	0.805
Celtic Sea, post-larvae	Present records	52	68.08	± 0.082	64-70	0.997
A. marinus						
Greenland	Jensen (1941)	38	69.39	± 0.195	67-72	1.204
Iceland	Bruun (1941)	97	71.53	± 0.112	68-73	1.104
Iceland	Kändler (1941, table 24, p. 120)	31	71.13	± 0.217	69-73	1.208
North Norway	Soleim (1945)	200	71.74	± 0.088	69-75	1.243
		168 (170)	72.06	± 0.088	69-74	1.145
		89	71.88	± 0.119	69-74	1.120
South Norway	Bergen	200	69.53	± 0.076	67-72	1.074
Faroes	Bruun (1941)	129	69.67	± 0.084	68-72	0.950
Northern North Sea	Raitt (1934)	205	69.21	± 0.079	67-72	1.131
North Sea, German Bight	Kändler (1941, table 24, p. 120)	67	69.75	± 0.124	67-72	1.015
Central Baltic, Pomerania		114	68.90	± 0.107	66-72	1.142
East Baltic, East Prussia		291*	68.50	± 0.066	65-72	1.135
Celtic Sea, post-larvae	Present records	45	68.56	± 0.128	67-70	0.858
Ammodytes species IV						
Celtic Sea, post-larvae	Present records	28	72.00	± 0.175	70-74	0.926
G. semisquamatus						
West Scotland and northern North Sea	Present records	51	68.16	± 0.127	65-70	0.901
A. dubius						
West Greenland	Jensen (1941)	179	75.10	± 0.082	73-78	1.099
West Greenland	Jensen (1944, p. 15, note 5)	53	75.07		?-80	

* This figure is given, evidently in error, as 191 in Kändler's paper.

row (p. 296) still persists when the denticles on the upper jaw appear (Pl. I, fig. 1c), and these in turn are still present when the adult character of the vomerine teeth appears in the later post-larvae.

For comparison with the vertebral counts of the post-larvae of this area (Table I), data obtained by other investigators from other north Atlantic areas are given in Table II.

Ammodytes tobianus

The number of *tobianus* post-larvae of stainable size was unfortunately small. There is, nevertheless, a significant difference between the mean number of vertebrae of the Plymouth post-larvae and of the adults from Exmouth and elsewhere. The excess, 2.18, of the Plymouth post-larvae over the Exmouth adults is more than five times its error: in fact the two populations appear to differ by at least 1.40. Until further data from this area are obtainable on the number of vertebrae in both the adults and post-larvae, this difference will remain something of an anomaly. The mean of the Exmouth sample is in keeping with the findings of other authors. But the mean of the post-larvae suggests, despite the smallness of the sample, that what are here taken to be *tobianus* do not in fact belong to the species. On the other hand, the pigmentation and time of occurrence of the post-larvae are characteristic of *tobianus*. The pigmentation of each individual was very carefully noted before staining and without exception was in full agreement with the figures and descriptions of Ford (1920) and Kändler (1941) (dark form, spring brood).

Ammodytes lanceolatus

Kändler's figures (1941, Table 23, p. 120) are the only published data from large samples on the number of vertebrae in adult *lanceolatus*. Their means are noticeably lower than the mean of the Celtic Sea post-larvae. As mentioned above, the identification of the post-larvae was confirmed by the denticles on the upper jaw and the pair of vomerine teeth.

Ammodytes marinus

The data for this species show the very considerable range of the mean number of vertebrae.

Mr P. A. Soleim informed us that his original data were not available; they were unfortunately lost during the course of post-war changes. The data in Table II relating to his samples of *marinus* were therefore calculated from careful measurements (in hundredths of an inch) of his published graphs (Soleim, 1945: fig. 7, p. 13 and fig. 10, p. 16). From the given total of specimens in each sample, the number at each different vertebral count was calculated, and hence the mean, standard deviation (σ) and standard error of the mean for each sample. In the Grense Jakobslev sample of 30 October 1939, the total number of specimens calculated from measurement is 168 instead of 170 as given by Soleim. This small discrepancy is unlikely to make any great difference in the ensuing calculations. In the other three samples, the totals calculated from measurement agree with those given by Soleim.

Ammodytes species IV

The nearest approach to the mean number of vertebrae of this post-larva occurs in adult *marinus* from northern Norway (Soleim's samples from Grense Jakobslev and Tana).

Data for *G. semisquamatus* and *A. dubius* are included for comparison with the foregoing species.

TABLE III. THE SEASONAL OCCURRENCE OF POST-LARVAL *AMMODYTES* SPP. IN PLYMOUTH WATERS IN 1930-31 AND 1935-37

Owing to loss and damage of some specimens, the monthly totals do not always agree with Mr F. S. Russell's original figures. The discrepancies are, however, not sufficient to distort the general results.

Monthly averages for the five years are shown in parentheses. The number of hauls per month are given under *A. lanceolatus* against the total of specimens taken in the month.

* denotes months in which a species occurred on the 1937-39 cruises.

	<i>A. lanceolatus</i>					<i>A. marinus</i>				
	1930	31	35	36	37	1930	31	35	36	37
Jan.	..	.. ⁶	.. ⁶	.. ⁵	.. ⁴	..	..	..	4	.. (0.2)
Feb.	.. ⁴	.. ⁴	.. ³	.. ³	4 ⁴ (0.3)	..	..	..	18	.. (1.2)
Mar.	.. ⁴	2 ²	5 ³	4 ⁴	30 ⁵ (1.9)	2	31	21	6	4 (5.1)
Apr.	.. ⁵	1 ⁵	8 ⁶	19 ⁴	12 ⁴ (1.86)*	..	..	..	..	.. *
May	4 ³	2 ⁴	16 ⁷	4 ⁴	21 ⁵ (1.86)*	..	..	..	..	..
June	4 ³	11 ³	4 ²	10 ⁴	5 ³ (2.2)	..	..	..	..	..
July	17 ⁵	15 ⁴	6 ⁶	14 ⁴	4 ⁴ (2.5)	..	..	..	..	..
Aug.	53 ⁴	5 ⁴	5 ⁴	4 ⁴	3 ⁴ (3.5)	..	..	..	..	..
Sept.	1 ⁴	3 ⁴	1 ⁵	.. ⁵	.. ⁵ (0.2)	..	..	..	..	..
Oct.	.. ⁴	.. ⁵	.. ⁵	1 ²	.. ⁴ (0.1)	..	..	..	..	..
Nov.	.. ⁴	.. ¹	.. ²	.. ⁴	.. ⁴	..	..	..	..	..
Dec.	.. ⁴	.. ⁵	.. ³	.. ³	.. ⁴	..	..	..	..	..

	<i>A. tobianus</i>					<i>Ammodytes</i> species IV				
	1930	31	35	36	37	1930	31	35	36	37
Jan.	..	..	..	..	..	..	..	3	28	85 (5.0)
Feb.	..	..	..	..	..	..	5	17	26	86 (5.4)
Mar.	..	..	..	..	..	9	35	53	13	37 (7.4)
Apr.	..	..	..	..	..	1	3	9	5	6 (1.0)*
May	..	1	..	..	.. (0.05)	1	..	..	..	.. (0.07)
June	..	1	..	..	.. (0.07)	..	..	..	..	..
July	..	1	..	..	2 (0.2)	..	..	..	..	..
Aug.	1	..	..	10	.. (0.6)	..	..	..	..	..
Sept.	..	1	8	3	.. (0.5)	..	..	..	..	..
Oct.	..	1	5	..	.. (0.2)	..	..	..	..	..
Nov.	..	..	..	..	..	..	..	..	..	2 (0.10)
Dec.	..	..	..	..	..	..	..	..	..	..

The March and August averages of *A. lanceolatus* are high owing to single large catches of twenty-seven and forty-seven specimens on 1 March 1937 and 7 August 1930 respectively. The January average of *Ammodytes* species IV is similarly weighted by a catch of eighty-two specimens on 27 January 1937.

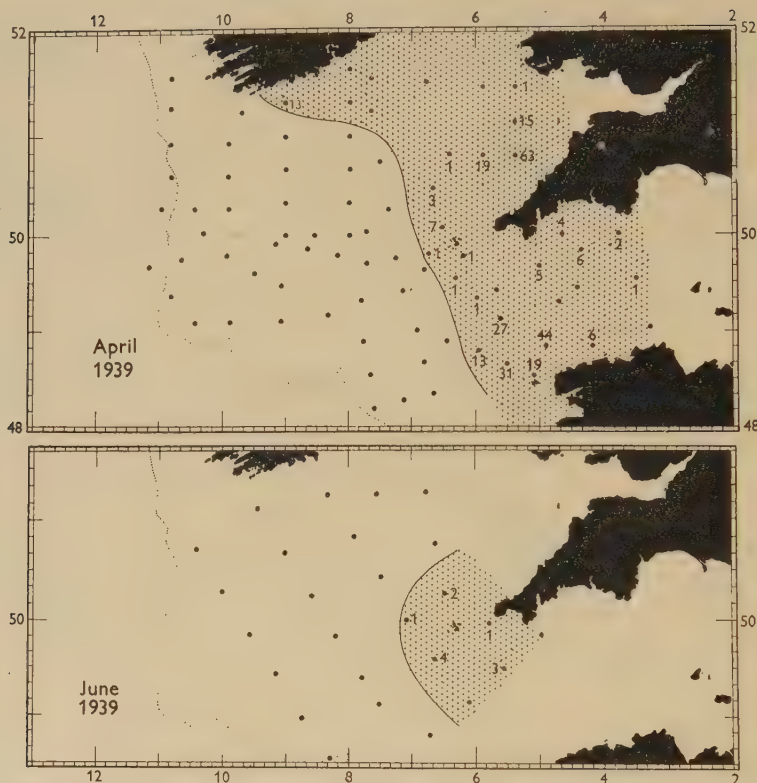
THE SEASONAL OCCURRENCE AND DISTRIBUTION OF THE POST-LARVAE

The seasonal occurrence of the four species of *Ammodytes* post-larvae in the Plymouth area in the years 1930, 1931 and 1935-37, together with the occurrences on the 1937-39 cruises in the Celtic Sea, is shown in Table III. It is evident that *A. lanceolatus* has a long spawning period lasting from early spring



Text-fig. 2. Distribution of post-larval *Ammodytes lanceolatus* in the Celtic Sea and Plymouth area in 1937 and 1938. Figures refer to the number of post-larvae caught at each station. The dotted line in this and succeeding figures indicates the 100-fathom contour.

until autumn (February-October) with a maximum in mid-summer. *A. marinus* spawns in winter and early spring (January-April). The spawning times of these two species are in agreement with Raitt's observations for Scottish waters (1934) and Kändler's for the North Sea and Baltic (1941). The com-



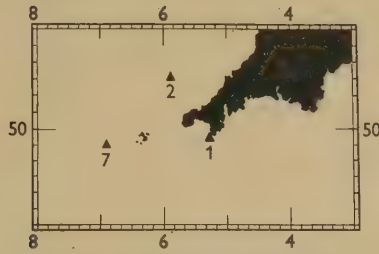
Text-fig. 3. Distribution of post-larval *Ammodytes lanceolatus* in the Celtic Sea and Plymouth area in 1939. Figures refer to the number of post-larvae caught at each station. No *Ammodytes* post-larvae were taken on the March 1939 cruise.

paratively few records of *A. tobianus* post-larvae point to a spawning period lasting from spring until autumn (April–October), with a maximum in August and September. In the North Sea and Baltic, Kändler (1941) found that *tobianus* has two pronounced spawning periods, in spring and in autumn. *Ammodytes* species IV, like *marinus*, starts spawning in winter, but continues rather longer—into early summer (January–May), and it may occasionally start in late autumn as is indicated by the record of two post-larvae in November 1937.

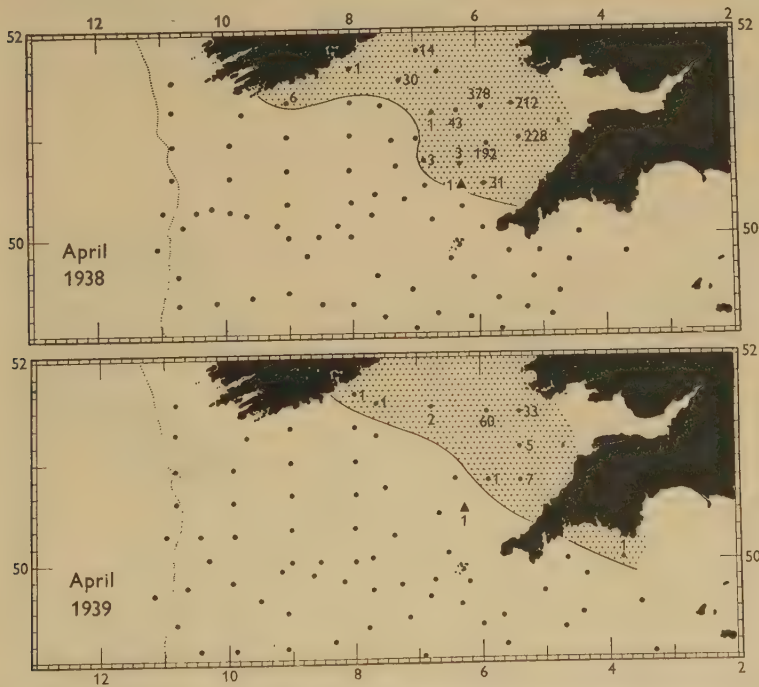
The numbers and distribution of the post-larvae taken on the 1937–39 cruises are shown in Text-figs. 2–6. For details of station numbers, positions, etc. see Corbin (1947), Figs. 1 and 2, pp. 67–8 and pp. 124–32.

No post-larvae were caught more than about 60 miles from land. They occurred in the eastern part of the Celtic Sea—at the western end of the English Channel and off the St George's and Bristol Channels—and not in the western area towards the edge of the Continental Shelf. The post-larvae

of *lanceolatus* (Text-figs. 2 and 3) and *Ammodytes* species IV (Text-fig. 6) were present throughout this region extending from south-west Ireland to the Brest Peninsula. The small number of *tobianus* post-larvae (ten specimens)

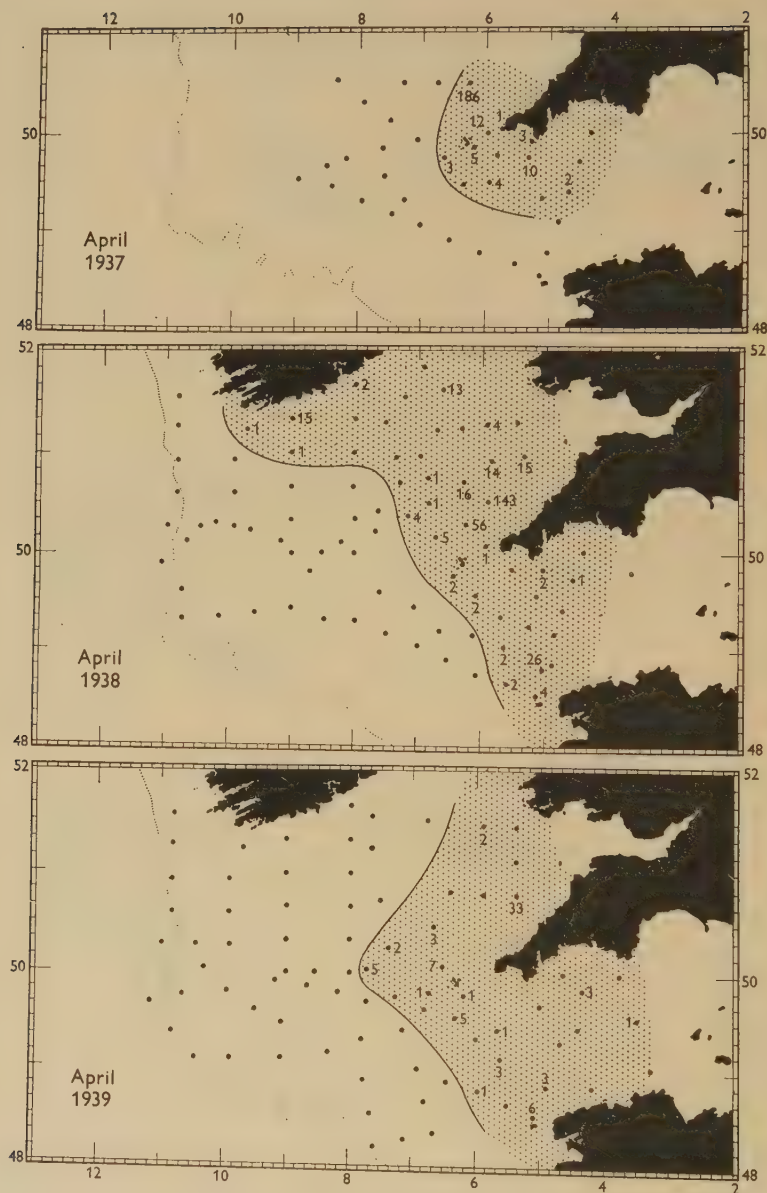


Text-fig. 4. Distribution of post-larval *Ammodytes tobianus* in the Celtic Sea in 1937-39. April 1937, Station 34 (one specimen); April 1938, Station 49 (two specimens); May-June 1938, Station 11 (seven specimens).



Text-fig. 5. Distribution of post-larval *Ammodytes marinus* in the Celtic Sea and Plymouth area in 1937-39. Figures refer to the number of post-larvae caught at each station. Station 32 of the April 1937 cruise, at which a single specimen was taken, is marked ▲ on both charts of this text-fig.

were all taken fairly close to land (Text-fig. 4). The distribution of *marinus* post-larvae was peculiarly restricted (Text-fig. 5). All specimens, with the exception of one taken off Plymouth (St. 62, April 1939), were caught in the



Text-fig. 6. Distribution of post-larval *Ammodytes* species IV in the Celtic Sea and Plymouth area in 1937-39. Figures refer to the number of post-larvae caught at each station.

north-eastern area—off the St George's and Bristol Channels. On the April 1938 and 1939 cruises, the species thus appeared to have a southerly limit of distribution along a line joining south-west Ireland and Land's End. The occurrence of only a single *marinus* post-larva on the April 1937 cruise is in agreement with this. It was taken about 35 miles north-west of Land's End (shown ▲ in both charts of Text-fig. 5), just on the southern limit of the *marinus* post-larva area of the April 1938 and 1939 cruises. All other stations of the April 1937 cruise were outside—to the south and west of—the 1938–39 *marinus* boundary. The presence each year of *marinus* post-larvae in the 1930–37 collections from the Plymouth area reveals, however, that they regularly occur there and confirms the single specimen taken off Plymouth (St. 62) on the April 1939 cruise. Kändler (1941) states that it may be concluded that the dispersal area of *marinus* ranges as far as the western end of the English Channel. It will be of interest to know from further observations whether the southern limit indicated by the April 1937–39 cruises should be continued across the western end of the English Channel from Land's End to, say, the Channel Islands. This would include the Plymouth area, but not the Land's End–Ushant region of the Channel mouth where none was taken at the numerous stations worked during the April 1937–39 cruises.

SUMMARY

The post-larval sand-eels (Ammodytidae) occurring in the Celtic Sea and Plymouth area are identifiable as *Ammodytes lanceolatus*, *A. tobianus*, *A. marinus* (not previously recorded from the area), and a fourth species of *Ammodytes*, the adult of which, it is concluded, is not yet known.

Adult *Gymnammodytes semisquamatus* (not previously recorded from the Plymouth area), the young of which are not yet known, increases the number of species in the area to five.

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APPENDIX

The earlier work of Ehrenbaum & Strodtmann (1904) and Ehrenbaum (1904, 1909) on the larvae and post-larvae of *Ammodytes* contains several errors of identification, due in part to the fact that *A. marinus* and its young stages were unknown at the time. The following notes attempt to correct the mis-identifications. Corrections already made by Ford (1920) and Kändler (1941) are also included.

Ehrenbaum & Strodtmann (1904)

Fig. 8, p. 104 (also Ehrenbaum (1909), Fig. 106*c*, p. 298), post-larva 20.5 mm.; ascribed to *A. tobianus*.

Kändler (1941) points out that the pigmentation and date of capture (February) of this specimen identify it as *A. marinus*.

Ehrenbaum (1904), Taf. VII

Fig. 70 (also Ehrenbaum (1909), Fig. 107*a*, p. 300), larva 4.2 mm. and Fig. 71, larva 5.1 mm.; both ascribed to *A. lanceolatus*.

The specimens were reared from artificially fertilized eggs. In these circumstances it seems very unlikely that an error would have occurred in the identification of the parents of the fertilization had they been specimens of *lanceolatus*. Neither of the larvae, however, shows the ventral fin-membrane pigment row which is specifically characteristic of the earliest stages of *lanceolatus* (p. 296), and the ventral gut pigment is also very much heavier than in early *lanceolatus*. The pigmentation is in all respects characteristic of *A. tobianus*. Both pigmentation and date of fertilization (June) rule out *A. marinus* and *Ammodytes* species IV.

Fig. 72 (also Ehrenbaum (1909), Fig. 107*b*, p. 300), post-larva 12.5 mm.; ascribed to *A. lanceolatus*.

Ford (1920) points out, and Kändler 1941 agrees with him, that the pigmentation of this specimen identifies it as *A. tobianus*.

Fig. 80, larva 2.2 mm. and Fig. 81, larva 4.0 mm.; both ascribed to *A. tobianus*.

These specimens hatched prematurely from artificially fertilized eggs. The date of fertilization (September) is therefore likely to be the only reliable criterion for identification, and indeed supports Ehrenbaum's identification.

Fig. 82, larva 4.5 mm.; ascribed to *A. tobianus*.

This specimen evidently resulted from the same artificial fertilization as those in figs. 80 and 81. Ehrenbaum's identification is thus supported by the date of fertilization. This and the lack of ventral gut pigment are in agreement with Kändler's (1941) lightly pigmented autumn-brood *tobianus* post-larva of the North Sea and Baltic.

Fig. 83, larva 4.7 mm.; ascribed to *A. tobianus*.

The specimen is figured from the dorsal side and cannot therefore be identified by its pigmentation. The date of capture (September) supports Ehrenbaum's identification.

Fig. 84 (also Ehrenbaum (1909), Fig. 106*a*, p. 298), larva 6.6 mm. and

Fig. 85, larva, anterior end; both ascribed to *A. tobianus*.

The date of capture (January) of these specimens, their pigmentation, the noticeably slender form, and particularly the length while still carrying a large oil globule (fig. 84, 6.6 mm.) are evidence that they belong to *A. marinus*.

Fig. 86 (also Ehrenbaum (1909), Fig. 106*b*, p. 298), post-larva 16.2 mm.; ascribed to *A. tobianus*.

Kändler (1941) points out that the pigmentation is clearly that of *A. marinus*.

It is of interest that Ehrenbaum and Strodtmann evidently did not procure any post-larvae of *A. lanceolatus*.

EXPLANATION OF PLATES I & II

The drawings were made from specimens preserved in formalin. All specimens are drawn to the same scale (see inset on Plates), with the exception of the specimen in Pl. I, fig. 2*a*. All specimens were taken in half-hour oblique hauls of the 2 m. stramin ring-trawl in the Celtic Sea or Plymouth area, with the exception of the specimen in Pl. I, fig. 2*a*.

PLATE I.

Fig. 1. *Ammodytes lanceolatus* Lesauvage

- a*. Post-larva 4.5 mm. Station L3-L4, Plymouth, 19. iii. 1937.
- b*. Post-larva 7.5 mm. Eddystone, 26. iv. 1937.
- c*. Post-larva 12.5 mm. Station 48, Celtic Sea, 25. iv. 1939.
- d*. Post-larva 18.5 mm. 4 miles SSE. of Mewstone, Plymouth, 22. vii. 1936.
- e*. Post-larva 26.5 mm. Eddystone, 13. vii. 1937.

Fig. 2. *Ammodytes marinus* Raitt

The scale for *a* is above the drawing. The scale for *b-h* is below *h*.

- a*. Larva 6.25 mm. Station 15(1), North Sea, 24. i. 1947, Cruise 3, R.V. *Platessa*, Hensen net, vertical.
- b*. Post-larva 7.5 mm. Station 46, Celtic Sea, 14. iv. 1938.
- c*. Post-larva 11.0 mm. Station 45, Celtic Sea, 14. iv. 1938.
- d*. Post-larva 14.0 mm. Station 45, Celtic Sea, 14. iv. 1938.
- e*. Post-larva 18.5 mm. Station 48, Celtic Sea, 25. iv. 1938.
- f*. Post-larva 19.0 mm. Station 45, Celtic Sea, 24. iv. 1939.
- g*. Post-larva 23.0 mm. Station 46, Celtic Sea, 25. iv. 1939.
- h*. Post-larva 27.5 mm. Station 45, Celtic Sea, 24. iv. 1939.

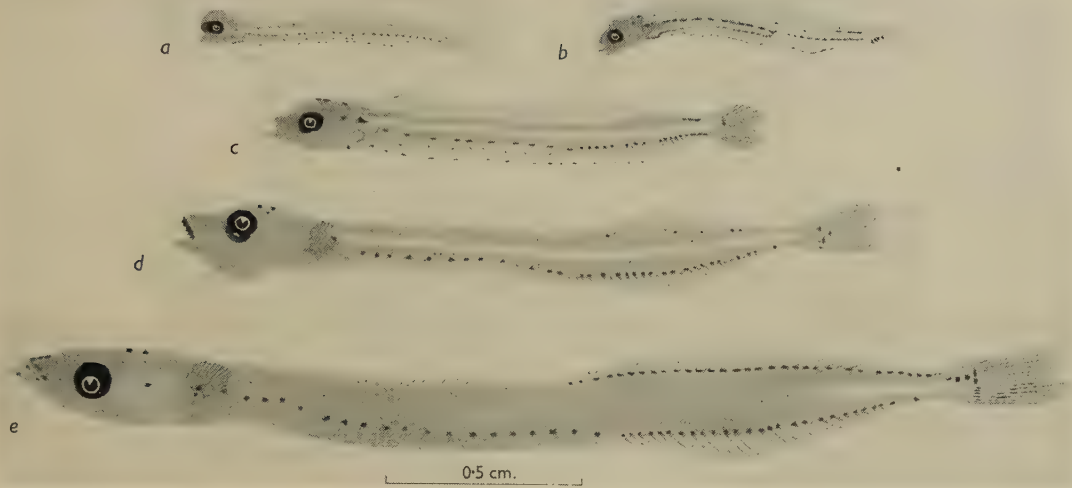


Fig. 1. *Ammodytes lanceolatus*

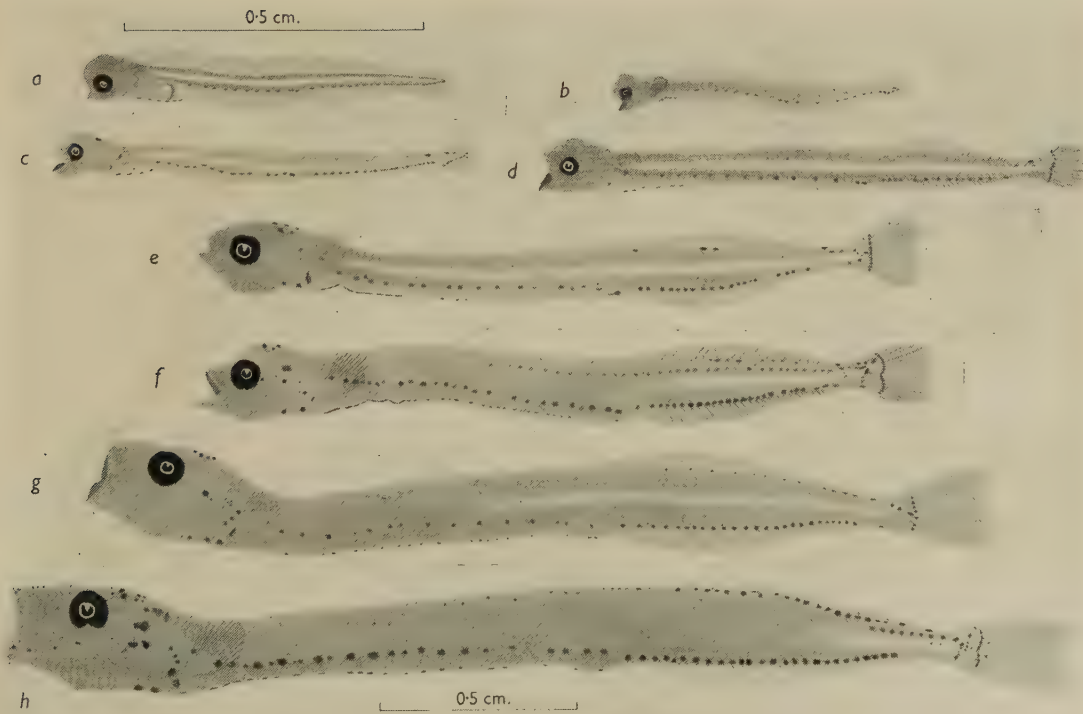


Fig. 2 *Ammodytes marinus*

del. V.V.

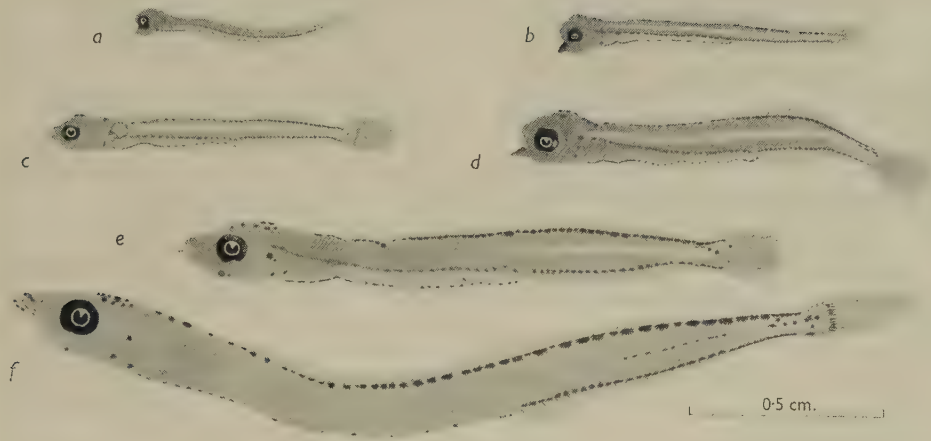


Fig. 1. *Ammodytes tobianus*

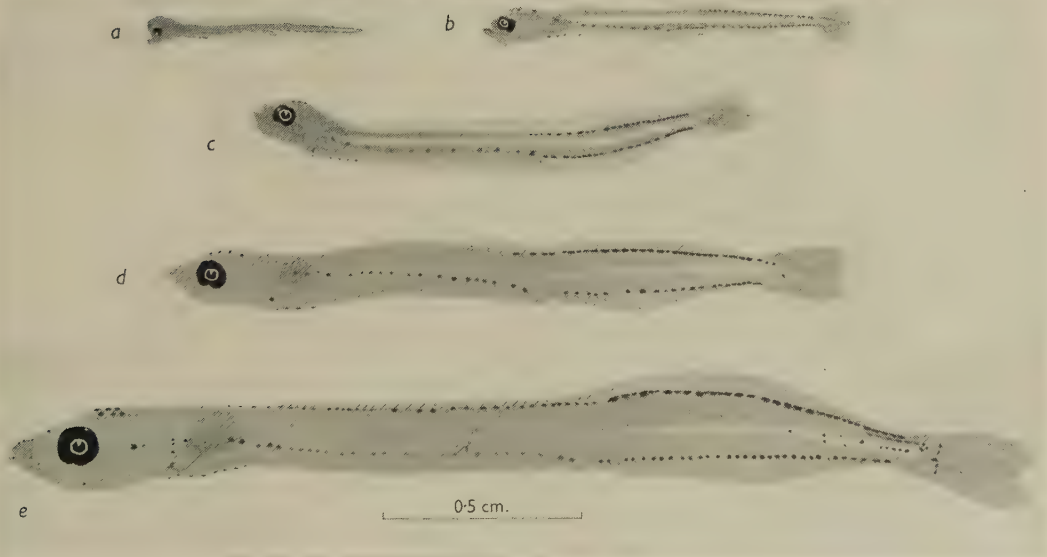


Fig. 2. *Ammodytes* species IV

del. V.V.

PLATE II.

Fig. 1. *Ammodytes tobianus* L.

- a. Post-larva 5.25 mm. Station 11, Celtic Sea, 2. vi. 1938.
- b. Post-larva 8.0 mm. Station 11, Celtic Sea, 2. vi. 1938.
- c. Post-larva 8.75 mm. Eddystone, 11. viii. 1936.
- d. Post-larva 11.0 mm. Eddystone, 24. vi. 1947.
- e. Post-larva 15.5 mm. Eddystone, 9. x. 1935.
- f. Post-larva 23.0 mm. Eddystone, 7. viii. 1930.

Fig. 2. *Ammodytes* species IV

- a. Post-larva 5.5 mm. Bolt Head E. x S.: Stoke Point N., Plymouth, 27. i. 1937.
- b. Post-larva 9.0 mm. Station 33, Celtic Sea, 20. iv. 1937.
- c. Post-larva 13.0 mm. Station 33, Celtic Sea, 20. iv. 1937.
- d. Post-larva 17.5 mm. Station 40, Celtic Sea, 23. iv. 1939.
- e. Post-larva 26.0 mm. Station 51, Celtic Sea, 25. iv. 1939.

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

PHOTOELECTRIC MEASUREMENTS OF THE SEASONAL VARIATIONS IN DAYLIGHT AT PLYMOUTH, FROM 1938 TO MARCH 1941, COMPARED WITH THE YEARS 1930 TO 1937

By W. R. G. Atkins and M. A. Ellison

Proc. Roy. Soc., A, Vol. 191, 1947, pp. 467-84

Measurements were made throughout with a vacuum sodium photoelectric cell and a Cambridge 'thread recorder'. The illumination during the last three years was below the average, but the three were closely similar. Of the eleven, 1930 was much the brightest, followed by 1934. The remainder were rather uniform. Of the eleven years May was brightest in six, June in four, July in one—1930. The mean value of the December illumination, found from the area of the intensity-time curve, is 1.37%, with May 15.61% and June 15.59%, calculated on the light of the year. The range of the monthly means lies between 20% for June and 59% for November.

There is no simple relation between the illumination integral and the number of hours of sunshine, rainfall, number of days with rain or wind direction. Calm days are never exceptionally bright; such days usually have wind force 3.

The illumination on days showing complete cloud cover throughout was during 1930 and 1936, 0.326 and 0.304 respectively of that on the brightest days, calculating on a month-to-month basis. Illumination on sunless days of 1930 was above that on similar days in 1936, a year of average illumination. On comparing Plymouth records with those got near Stockholm by Aurén it is seen that similar wide ranges in light intensity, within the same month, were found in both.

W.R.G.A.

NOTE ON THE SPECTROSCOPIC AND BIOLOGICAL DETECTION OF POTASSIUM IN SEA WATER AND 'POTASSIUM-FREE' ARTIFICIAL SEA WATER

By W. R. G. Atkins

Journ. Conseil, Vol. XV, 1948, pp. 169-72

Using sea water evaporated in silica dishes Moore and Philpot of Scientific Instrument Research Association showed lines 4044 and 4047 Å were less effective for detecting potassium than were 7699.0 and 7664.9 sought on F. Twyman's advice. After reducing glare by careful cleaning the latter pair

were detected in sea water supposedly potassium free. Glare was best eliminated by a selenium red glass. In the 'potassium free' water the ratio of potassium to sodium by weight was about 7 to 100 million, as found by a biological method of analysis. When the water was exhausted by maximal diatom growth potassium was still detectable spectroscopically in the filtrate, but this is not diatom free and accidental breakage of a centrifuge tube may have liberated some potassium. War prevented further work. W.R.G.A.

DAYLIGHT AND ITS PENETRATION INTO THE SEA

By W. R. G. Atkins

Trans. Illuminating Eng. Soc. (London), Vol. X, No. 7, 1945, 12 pp.

A lecture delivered at the Annual General Meeting of the Society, summarizing work on the variation of daylight throughout the year and with latitude; the measurement of submarine illumination; and the consequent changes in the phosphate and oxygen of the sea which give a measure of the production of phytoplankton. W.R.G.A.

A SUGGESTED REPELLENT FOR SCHISTOSOME CERCARIAE

By W. R. G. Atkins

Journ. Hygiene, Vol. 45, No. 4, 1947, p. 468

Attack by cercariae of *Schistosoma haematobium*, *S. mansoni* and *S. japonicum* causes in man debilitating diseases which in certain countries are widespread. Infection is mainly through the skin. In U.S.A. and Canada a dermatitis only is caused by cercariae liberated from *Stagnicola emarginata* and other fresh-water snails. Possibly copper oleate, stearate or palmitate might be effective repellents when applied in 1-5% dilution in mineral jelly or crude lanoline for cercariae and could be tried first against the relatively harmless species. Such copper compounds have been useful as anti-fouling agents and preservatives for ropes, etc. W.R.G.A.

THE NUTRIENT BALANCE IN THE SEA

By L. H. N. Cooper

Research, Vol. I, pp. 242-7

The interdependence of changes in the chemical composition of sea water and of variations in plant and animal production is reviewed. The account, not intended to be 'popular', is largely based on papers published from the Plymouth Laboratory during the past twenty-five years. L.H.N.C.

THE DISTRIBUTION AND BIOLOGY OF HAKE

By T. John Hart

Biol. Rev. Vol. 23, 1948, pp. 62-80

Recent advances in our knowledge of the general biology, taxonomy and economic importance of the genus *Merluccius* are described by way of introduction to a detailed discussion of its distribution.

It is shown that all the species conform to the same distributional pattern in relation to major hydrological features, within the limits of their normal range. Where relatively cold currents flow towards the equator in the warmer half of the normal habitat of any one of these species, its range is extended in that direction; but if a relatively warm current is flowing pole-wards, the range in the direction of the equator is restricted. In the colder half of the normal habitat of each species the converse relationship holds good.

Surface isotherms have been used as the most reliable general criterion symptomatic of the environmental complex that leads to this type of distribution because in many parts of the world more detailed hydrological data are not yet available; but it is emphasized that other factors, more or less intimately interrelated with the direct effect of temperature, are also involved.

The distribution of the genus offers a good example of the wider aspects of the phenomenon of 'organic polarity' discussed by Wimpenny (1941), while the bionomics of the better known individual species show some more detailed aspects of it with great clarity.

T.J.H.

THE GIANT NERVE-FIBRES IN THE CENTRAL NERVOUS SYSTEM OF *MYXICOLA*
(POLYCHAETA, SABELLIDAE)

By J. A. C. Nicol

Quart. Journ. Micr. Sci., Vol. 89, 1948, pp. 1-46

A study of the giant axon in the central nervous system of *Myxicola infundibulum* has shown that this structure possesses many peculiar features. It occupies a large volume of the nerve cord and extends throughout the length of the animal. Its diameter is greatest anteriorly, about 1 mm., and tapers off posteriorly. In each segment it gives off branches to the longitudinal muscle fibres in the body wall. The giant fibre is connected with nerve cells in the supra-oesophageal ganglia, and with nerve cells in each segment. It is concluded that the giant fibre of this animal is a large syncytial structure extending throughout the nervous system and body wall.

Added evidence for its syncytial nature has been adduced by cutting it and examining the axon after 16 days. The giant axon failed to degenerate in front

of or behind the cut owing to the existence of nerve cells at all levels. The giant axon is similar in the related species, *M. aesthetica*.

The large diameter, rapid conduction velocity, and through nature of the axonic pathway have been correlated with the sedentary mode of existence and quick withdrawal reflex of these animals, and are regarded as having survival value.

J.A.C.N.

PURE AND ALLIED SCIENCE OF THE SEA
(being the Ludwig Mond Lecture, delivered at the University of
Manchester on 11 March 1948)

By F. S. Russell

Science Progress, Vol. XXXVI, 1948, pp. 423-35

Some aspects of marine research are reviewed historically to show how advances in our knowledge of the sea have been much influenced by the interdependence of pure and applied science.

F.S.R.

FURTHER EXTENSION OF THE RANGE OF *CREPIDULA FORNICATA* (L.)

By G. M. Spooner

Journ. Conchology, Vol. 22, 1947, p. 243

During the war years the Slipper Limpet, *Crepidula fornicata* (L.) spread into Weymouth Bay and by 1946 had become a dominant member of the fauna. In spreading westwards down the English Channel coast, the species had taken about twenty years to cross the gap between Studland Bay and Weymouth Bay.

G.M.S.

THE BRITISH SPECIES OF PSENINE WASPS (HYMENOPTERA: SPHECIDAE)

By G. M. Spooner

Trans. R. Ent. Soc. London, Vol. 99, 1948, pp. 129-72

Existing knowledge of the British species of the genera *Psenulus*, *Psen*, and *Mimesa* (slender fossorial wasps which prey on aphides and jassid plant-bugs) is summarized, covering both taxonomy and general biology. Much hitherto unpublished matter is incorporated, including records of prey kindly supplied by Dr O. W. Richards. New identification keys for the two sections of *Mimesa* are given. *M. bruxellensis* Bondr. is recorded as British for the first time, and *M. celtica*, a form inhabiting sand dunes in the west, is split off from *M. unicolor* (Lind.) as a new species.

G.M.S.

REPORT ON THE SEA FISHERIES OF SIERRA LEONE

By G. A. Steven

London: Crown Agents for the Colonies, Millbank. 1947. 66 pp.

This Report is based on work carried out by the author on behalf of the Government of Sierra Leone for their guidance in developing the fisheries resources of the colony. It includes a survey of the methods of fishing already fully established, together with recommendations for their improvement. The results of experiments with methods new to that region, e.g. trawling and trammel-netting, are also described. Trials with a motor trawler based on Freetown gave very encouraging returns in regard to both the quantity and quality of fish available.

Most of the work was done during the recent war when fishing gear was hard to obtain. Ropes and twines made by hand by the natives themselves from local fibres had largely to be used but proved unsatisfactory. A hand-operated ropemaking machine was therefore introduced and local fishermen taught to use it. This proved a great boon and saved the beach-seining industry from collapse in particularly difficult times.

Fish preservation and transportation are two problems of special difficulty and importance in tropical regions. Native methods are crude and effective for only short periods. Recommendations are therefore made for exhaustive and prolonged experimentation so that new and improved techniques, appropriate to the commodity and the climate, may be devised and perfected. Particular attention is directed to the potentialities of dehydrated fish products for native use.

The report concludes with proposals and recommendations for the formation of a Fisheries Department, and the building of a local Fisheries Laboratory on a site already available on the outskirts of Freetown. The difficulty of recruiting well-qualified and adequately trained staff is fully realized, but it is pointed out that even a single energetic and competent fisheries biologist, assisted by educated and intelligent native helpers, backed by an enlightened public and supported by courageous Government policy, could do much to plan, prepare and initiate further development.

G.A.S.

THE BRITISH RAIIDAE

By G. A. Steven

Science Progress, Vol. XXXV, 1947, pp. 220-36

Fishes of the genus *Raia* (Rays and Skates) collectively make an important contribution to the total landings of British food fishes. Just over a dozen species occur in British waters, and of these no less than eleven are present on the fishing grounds around Devon and Cornwall where they are caught with

little variation in numbers over the whole year. This indicates a minimum of migratory movement which is strikingly confirmed by marking experiments. In over 60% of the recaptures of marked *Raia clavata* (on which most work has been done) the fish were caught in precisely the same place as they were liberated, after periods varying from 12 days to over $3\frac{1}{2}$ years. Because of this, the same fish can often be recaptured several times after marking. The record so far is held by a fish living in a depth of 25 fathoms that was captured five times within a year.

It is found that on the various grounds where different kinds occur there is a fairly rigid segregation of the species and at certain times, a segregation also of the sexes.

Growth rates have been obtained for *Raia clavata*. In fishes over a size-range of 20-50 cm. disc width an increment of from 4 to 8 cm. in width takes place in one year, chiefly in the summer and autumn. Male fish reach maturity when about 7 years of age but females are several years older before becoming sexually mature.

G.A.S.

BOOK NOTICE

THIS GREAT AND WIDE SEA

By R. E. Coker

The University of North Carolina Press: Oxford University Press, 1947. Price 27s. 6d. net

The theme of this American book is the salt water of the whole wide world. Between the covers of one normal-sized volume the author moves in a broad steady sweep from the chemistry and physics of sea water on through the pasturage of the sea, and the many ramifications of the animal life it sustains, to that final crowning manifestation of metabolic efficiency, the growth rate of whales. The book is divided into three parts: the first of these summarizes the history of oceanography and the major expeditions, with some account of the great oceanographers and marine biologists of the past, not forgetting mention of the marine stations scattered thinly and irregularly round the borders of the great ocean basins whose topography is briefly considered. The second part comprises seven chapters devoted to the chemistry and physics of sea water, the bottom deposits, oceanic circulation and the tides, and the heating effect of the sun on the sea. The third and longest part surveys the plant and animal life, the plankton, benthos and nekton, the variations in structure and habit, adaptations and interrelations. With an ease of style and wealth of illustrative detail this overall review of the oceans and the life they contain gives to the student a well-proportioned, up-to-date, and sound framework of knowledge on which to build, while the experienced worker in some corner of the field will find himself refreshed and stimulated by it.

It is a pity that a text so informative and well balanced should not be more worthily illustrated. The ninety-one half-tone plates are a very mixed bag, some good, some bad and many indifferent. A few have relatively little bearing on the text, some are new and interesting, but far too many are of poor quality photographically and unworthy of inclusion. It is to be hoped that in a future edition these half-tone insets will be drastically revised and better printed. A few more carefully chosen line drawings would enliven the text and increase its attractiveness to the general reader. Some indication of scale should be given to the drawings of various microscopic and other organisms at present included.

D.P.W.

A NEW BOTTOM-SAMPLER

By N. A. Holme, B.A.

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(Plate I and Text-figs. 1-4)

INTRODUCTION

At Plymouth the bottom-fauna is usually sampled by the trawl and dredge, but for quantitative work the $\frac{1}{10}$ m.² Petersen grab is sometimes used. Allen (1899) surveyed the bottom-fauna, on grounds between the Eddystone and Start Point, by means of trawling and dredging only. Ford (1923) has made collections of the bottom-communities near Plymouth, and gives lists showing the densities of species taken with the Petersen grab. Steven (1930) also used this grab for a survey of a limited area, but Smith (1932) resorted to a conical dredge with canvas bag, having found the grab ineffective in shell-gravel.

Davis (1925) has attempted to analyse some of the inaccuracies due to sampling with the grab. To some extent variations in the fauna in successive hauls are due to a patchiness of the fauna in any one soil, and also to the patchy distribution of soils in any one area. Rolling of the ship affects the size of the sample by altering the rate at which the grab hits the bottom and hence the size of the 'bite'. Drifting of the ship tends to decrease the size of the sample, as the grab must be pulled vertically from the soil to take its maximum 'bite'. The volume of the sample also depends on the consistency of the soil, which will affect not only the depth to which the jaws penetrate, but also the amount of material lost during hauling. Thus Smith (1932) found that when sampling on shell-gravel the grab frequently came up almost empty, the jaws having failed to close because of pieces of shell wedged between the teeth.

A further source of error is emphasized by Steven (1930): this is the ability of certain species to evade the grab, either by active burrowing or by normally living at a depth beyond its reach.

Thamdrup (1938) gives an account of the van Veen bottom-sampler, which differs from the Petersen grab by having long arms to the ends of which are attached the cables actuating the closing movement. A considerable leverage effect is thus exerted to close the jaws. In addition, the instrument is probably less likely to leave the bottom prematurely if there is a sudden jerk on the cable due to rolling of the ship. On a sandy bottom the van Veen sampler takes two or three times as much soil per unit area as does the Petersen grab.

Knudsen (1927) describes an ingenious sampler capable of digging to a depth of 30 cm. in sand. Comparable hauls against the Petersen grab (see Johansen,



1927) showed that it brought up ten to twenty times as much soil and four to five times as much animal tissue (by weight) as the latter. This instrument would hardly be suitable for use in the open sea in its present form owing to the risk of loss of material during hauling.

A new sampler has been designed to overcome some of the difficulties of bottom-sampling in the Plymouth area. These may be summarized as: the coarseness of the deposits, which makes penetration difficult and tends to result in considerable loss while hauling; Atlantic swell which makes perfectly calm days rare, so that the speed with which the sampler hits the bottom is variable; and currents which cause the sampler to descend rather obliquely, whether the ship is anchored or not.

I am indebted to Dr H. W. Harvey, F.R.S., and Mr G. A. Steven for suggestions and criticism in the design of the apparatus, and to Mr F. G. C. Ryder for constructing a working model of the grab and for help in many ways. I am also grateful to Captain C. Hoodless and the crew of R.V. *Sabella* for their skill in working the sampler at sea.

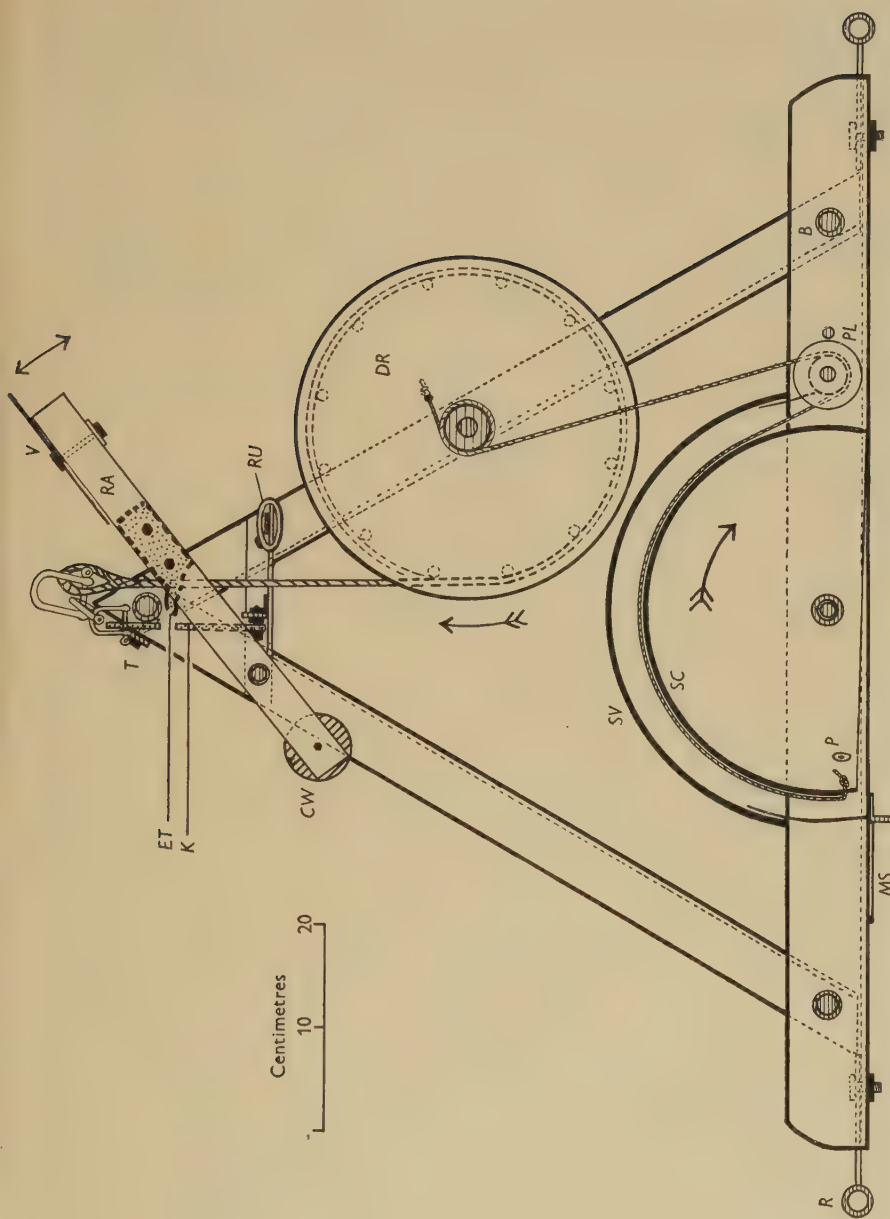
This work was accomplished during the term of a D.S.I.R. Research Grant at the Plymouth Laboratory and I am grateful to the Director and staff for facilities offered me during this period.

Mr F. S. Russell, F.R.S., Mr G. A. Steven and Mr E. Ford have kindly read the manuscript and have made a number of helpful suggestions.

The echinoderms shown in Table I were kindly identified by Mr H. G. Vevers, and some of the molluscs by Miss U. M. Grigg.

THE SAMPLER

This is shown in Text-fig. 1 and in Pl. I, fig. 2. It consists of a frame supporting a semicircular scoop (sc), which rotates through 180° to take a sample. The scoop is actuated by unwinding cable from a large drum (DR) by the side of which is a smaller drum, which winds in a thin cable attached to the scoop. By this means a considerable mechanical advantage is obtained, so that the upward pull on the cable required to close the apparatus is small. Since there is only a single scoop there is no risk of the jaws not closing, and washing out during hauling is probably small, judging by the appearance of the sampler when it is coming up just beneath the surface. The sample is protected by a semicircular cover (sv), but there is a slight loss of soil when the grab breaks the surface and water empties from it. The sampler weighs rather more than 45 kg., and in use it is weighted to about 110 kg. The theoretical size of the 'bite' is a rectangle of $\frac{1}{20}$ m.² surface area, semicircular in section, with a maximum depth of 15 cm. Some animals undoubtedly live below this depth, but observations on the shore and in baths of sand indicate that a very much greater force is required to dig deeper than this.



Text-fig. 1. Side view of the sampler, seen as if the frame on one side were removed. The key and the engaging tooth are stippled. B, frame bolt and distance piece; CW, counterweight; DR, drum; ET, engaging tooth; K, key; MS, transverse metal sheet; P, hole for wooden peg; PL, pulley; RA, release arm; RU, metal strip protected by rubber hose; SC, scoop; SV, scoop cover; T, cross-piece holding key in position; V, vane.

The apparatus resembles in some respects the dredge used by Stetson (1938) for taking a small semicircular core of bottom-sediments. Since the design of the sampler was liable to alteration it was largely constructed by bolting rather than welding. The only parts requiring to be made professionally were the large ring, the drum, the scoop, and the scoop cover.

DETAILS OF CONSTRUCTION

The frame consists of six pieces of heavy angle-iron, bolted to form two triangles separated at their bases by 17 cm. and at the top by a slightly greater distance. The two sides of the apparatus are joined by bolts and distance-pieces of iron piping ('gas-pipe').

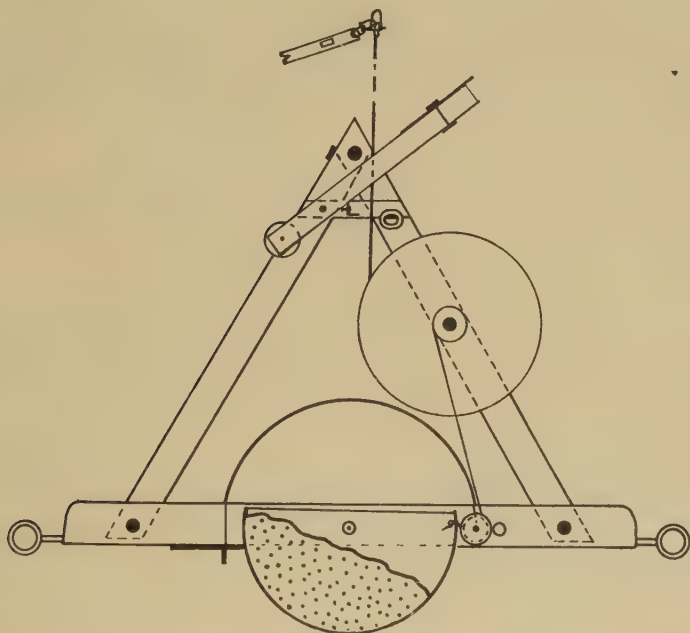
The ring (R) is of iron piping, attached to the base of the frame by welded lugs and bolts. The function of the ring is to keep the grab level on the seabottom, and also to prevent it damaging the ship's side.

The scoop (SC) is of steel plate 3 mm. thick welded to form a parallel-sided semicircular structure of external radius 17.5 cm. and width 15 cm. At the centre is welded a length of iron pipe through which passes an iron bar on which the scoop rotates. The bar is removed when the scoop is to be emptied. The cable attached to the small drum is fastened through a hole at one end of the scoop. During the descent the scoop is kept in an inverted position by a small wooden peg (P) passing through a hole in the scoop and the frame: this is sheared off when digging commences. The cutting end of the scoop is filed to a rather blunt edge. (Another scoop is being tested which has a pair of long teeth which precede the scoop and may help to anchor it in the soil.) While digging, the scoop tends to pile up soil in front of itself, but this falls back into the scoop when it is closing. There may be a slight loss of this soil through the gap between the scoop and the frame. Thus any stratification in the soil is partially disrupted. Outside the arc of the scoop the soil is prevented from piling up by the wide frame-base and a transverse sheet of metal (MS) pressing down on the soil surface. The arrangement of parts during hauling is shown in Text-fig. 2. The thin cable passes over the top of the scoop, round a pulley (PL), and is attached to the small drum on to which it is wound when the scoop closes. Should the scoop be unable to close, owing perhaps to catching on a piece of rock, a force of over 500 kg. is exerted on this cable, which is sufficiently thin to break and thus free the scoop. In practice the axle of the pulley tends to bend owing to the force exerted on it when the scoop is cutting through shells, etc., and this has had to be replaced by a thicker bar.

The large drum (DR) consists of two circular sheets of iron between which are welded short lengths of iron bar on which the large cable is wound. The latter is 3.5 m. in length and 25.5 mm. circumference. It is secured at one end to the centre of the drum by a shackle and short length of chain (these are not shown in Text-fig. 1). During hauling the cable has completely unwound from the large drum (to which it is still attached by the chain) so that there is

no longer any tension on the thin cable. The upper end of the cable passes between the top bolt of the frame and a metal strip protected by a piece of rubber hose (RU). It is attached to the 'key' (K) of the release through three shackles and to a cable from the ship of 32 mm. circumference.

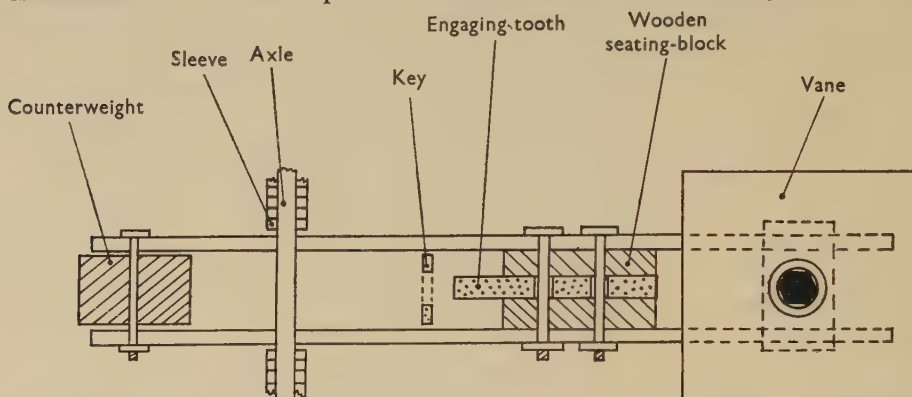
During the descent the weight of the apparatus is taken by the key. The key is a short length of thick metal strip with a slot in which the engaging tooth on the release arm grips during descent. The lower end of the key has a notch which slides on to a bolt head, thereby keeping it in position. The key is



Text-fig. 2. Position of parts when the instrument is closed. The soil sample is stippled.

prevented from lateral movement in one direction by the sides of the release arm, and in the other by the top bolt of the frame and a transverse metal strip (T). The release arm (RA), shown also in Text-fig. 3, consists of two metal strips separated by about 45 mm. internally. The engaging tooth (ET) is held between the strips, gripped between two blocks of hard wood. The base of the engaging tooth is slotted to allow adjustment of its position relative to the arm. The release arm pivots on an axle, being counterweighted so that the long arm just tends to drop. During descent it is kept in the upward position by the force exerted on the engaging tooth. When the sampler reaches the bottom the cable slackens, the arm drops and the key can slide out while cable is unwound from the drum. A vane (V) has been fitted to one end of the arm, as was done by Stetson (1938), to minimize the chances of release if the cable should momentarily slacken while the grab is descending. The release has proved

most successful, and only occasionally fails to work. The key is kept to a minimum size as it has to pass over a roller-sheave while hauling.



Text-fig. 3. Top view of the release arm. Transverse bolts are shown in section. The key and engaging tooth are stippled. The sleeves prevent lateral movement of the arm on its axle.

METHOD OF USE

The sampler is hoisted by a cable attached to the winch and passing over a roller-sheave on the boom, the latter being swung over the ship's side (Pl. I, fig. 1).

The routine while sampling is as follows. The cable is wound on to the large drum and the release set, strain being maintained by taking some of the weight on the ship's cable. The scoop is placed in the 'closed' position, and its axle inserted. It is then rotated backwards to the 'open' position, care being taken that the thin cable winds straight across its top. The peg is inserted and the apparatus lowered over the side. As soon as the cable slackens, hauling commences. The cable need not be vertical while the sampler is closing, as the latter is extremely stable on the bottom. Since the efficiency of the sampler does not depend on the force with which it strikes the bottom, it may be lowered at any speed.

When the sampler is on board again, the cable is immediately rewound on to the large drum and the release set. The scoop is then removed and emptied. This is less damaging to the animals than merely inverting the scoop *in situ*.

In a depth of 30 m. a sample can be taken every three minutes.

A 'safety rope' is often used to minimize the risk of loss. This is attached from the end of the ship's cable to the ring. In common with all heavy gear, the sampler is difficult to work in a moderate sea.

RESULTS

During 1948 the new sampler has been used at sea on a number of occasions, and in August a total of 100 hauls were made at thirty-seven stations during a cruise in Great West Bay. This provided a fair test of the instrument in

continuous use under favourable sea conditions. On the whole the instrument has worked successfully, and has taken good samples on sands, fine gravels and muds: adequate hauls have been taken at nearly all stations so far attempted.

The maximum volume of a sample is about $5\frac{1}{2}$ l. In practice the scoop is seldom quite full, usually bringing up 3–4 l. of soil. A number of hauls with this instrument and with the Petersen grab have been made to show the comparative increase in sampling efficiency. Sample volumes were:

Muddy gravel off Mewstone. Ship anchored.

New sampler: 5.25, 5.6, 5.25 l. in successive dips, i.e. average of $10.7 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

Petersen grab: total of 8 l. in three dips, i.e. $2.67 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

Muddy sand in Bigbury Bay. Ship anchored.

New sampler: first five dips—12 l., i.e. $c. 4.8 \text{ l.}/\frac{1}{10} \text{ m.}^2$; second five dips—11 l., i.e. $c. 4.4 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

Petersen grab: five dips—1 l., i.e. $0.2 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

Muddy sand in Cawsand Bay. Ship anchored.

New sampler: first five dips—10.75 l., i.e. $4.3 \text{ l.}/\frac{1}{10} \text{ m.}^2$; second five dips—10.5 l., i.e. $4.2 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

Petersen grab: five dips—1.75 l., i.e. $0.35 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

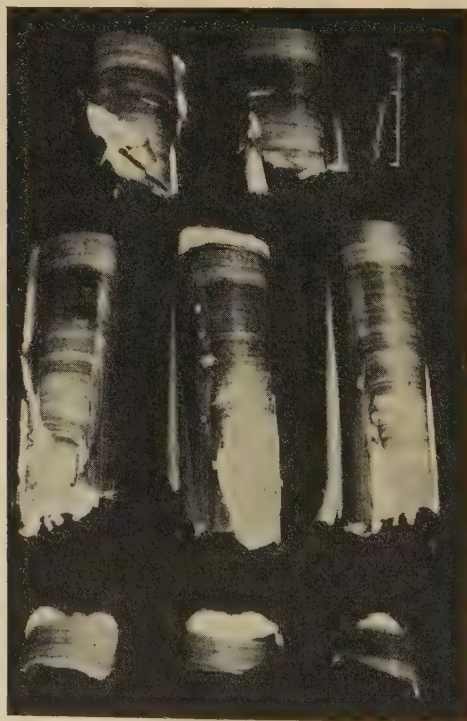
Johansen (1927) made a similar comparison between the Knudsen and Petersen grabs. On sand the former brought up an average of 25.6 l., whereas the Petersen grab only collected an average of $1.2 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

Thamdrup (1938) gives a number of comparisons of the van Veen and Petersen grabs. In a typical haul, in sand, the former brought up 3.4 and the latter $1.7 \text{ l.}/\frac{1}{10} \text{ m.}^2$.

The collections made in Bigbury Bay show that the new instrument samples the bottom-fauna more efficiently than does the Petersen grab. The results of collections of 0.5 m.^2 area are given in Table I. It will be seen that for nearly all species the Petersen grab gives too low a figure. In addition, only five species were recorded as against thirteen with the new sampler. It must be emphasized that this soil, being very tightly packed, is most unfavourable for bottom-sampling, and that on other grounds the differences in sampling efficiency would be rather less. The depth to which the various instruments were digging is indicated by fragments of *Ensis* shells taken (Text-fig. 4). The Petersen grab failed to capture any individuals, possibly because its jaws were not powerful enough to cut through the shell; while the new sampler cut off three individuals about 8 cm. from their upper ends, and shorter lengths of two other specimens. A dredge haul over the same ground cut off the top 2 cm. of three individuals. Assuming that the tops of the shells lie near or at the surface of the sand, and that the animal burrows nearly vertically,

TABLE I. COMPARISON OF HAULS MADE IN BIGBURY BAY,
18 MAY 1948. MUDDY SAND, SHIP ANCHORED

Instrument ...	New sampler	New sampler	Petersen grab
No. of dips	5	5	5
Total area (m. ²)	0.25	0.25	0.5
<i>Nephtys</i> sp.	2	c. 4	1
<i>Magelona papillicornis</i>	c. 73	c. 50	2
Cirratulid	—	—	1
Gephyrea	1	—	—
Annelids <i>indet.</i>	10	7	—
<i>Cellaria</i> sp.	—	—	1
Cumacea	3	4	—
<i>Bathyporeia elegans</i>	71	27	28
Amphipods <i>indet.</i>	2	1	—
<i>Natica alderi</i>	1	3	—
<i>Cylichna cylindracea</i>	4	—	—
<i>Macra corallina</i>	—	1	—
<i>Ensis</i> ? <i>siliqua</i>	4	1	—
<i>Amphipholis squamata</i>	2	—	—
<i>Echinocardium cordatum</i>	1	—	—

Text-fig. 4. *Ensis* from Bigbury Bay. Top two rows: individuals caught in new sampler; bottom row: individuals caught in dredge. For further explanation see text. The scale is 3 cm. long

the new sampler would seem to be digging about 8 cm., which is consistent with the volume of sand (c. $2\frac{1}{2}$ l.) brought up.

DISCUSSION

In the last section it was shown that the new sampler is very much more efficient than the Petersen grab as a quantitative sampler on certain grounds in the Plymouth area. Other workers have compared the Knudsen and van Veen samplers against the Petersen grab and have also found that better results were obtained, when working on a sandy bottom.

While the Petersen grab is no doubt suitable for working in sheltered waters and on a soft muddy bottom, it is clearly relatively inefficient on a hard bottom. It has, however, been used by a number of workers under the latter conditions and has been found a useful instrument for semi-quantitative evaluation of the benthos. The variability in the size of sample taken on any one ground and on different grounds is in itself sufficient to show its unreliability in making an accurate estimate of biomass.

The Knudsen sampler, which digs to a depth of 30 cm., has shown the need for sampling to a considerable depth in order to capture the deeper-burrowing invertebrates. The use of the Knudsen sampler is, however, restricted on account of its weight (about 200 kg.), and its inability to dig into deposits other than sand.

The van Veen sampler is a considerable improvement on the ordinary type of grab, as judged by the volume of sample brought up. But there is still some risk of losing material through stones becoming wedged in the jaws.

The new sampler was designed to take a sample of sand or gravel which should be subject to the minimum of loss during hauling. In addition, it has been shown to dig considerably deeper than the Petersen grab, and to the same order of depth as the van Veen sampler. The area sampled ($\frac{1}{20}$ m.²) is, however, rather small, and the apparatus rather heavy, and so difficult to work except in calm weather.

One of the most serious drawbacks to maximum efficiency appears to be the lateral shifting of the frame while the scoop is digging; this causes a decrease in sample volume. The addition of extra weights appears to be of little advantage in stopping this movement, and it is suggested that the only solution is a grab with two scoops working independently and rotating in opposite directions. The alternative of spikes or cross-pieces of angle iron on the base of the frame, to increase the grip on the soil, has not been very successful, as these tend to damage the ship's rail and do not seem to increase the size of the sample appreciably.

A half-scale model made in wood proved to be successful and took samples of about 300 c.c., being worked by hand from R.L. *Gammarus*. It is suggested that a sampler of this size might be used for survey purposes where a rather larger volume than that obtained by the 'snapper' is required.

SUMMARY

A bottom-sampler is described for use under open-sea conditions, particularly where the bottom is of sand or coarser material.

It takes a sample of $\frac{1}{20}$ m.² area of semicircular cross-section and maximum depth 15 cm. There is probably little loss of material while hauling and no danger of the apparatus losing soil through being wedged open by shell fragments, etc. The instrument weighs over 45 kg. and is weighted to 110 kg. in use.

Comparable hauls have been made against a Petersen grab: the new sampler digs four or five times as deep on a sandy bottom, and is thus of similar efficiency to the van Veen sampler. It is probably more efficient, however, than either of these on a bottom of fine gravel.

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EXPLANATION OF PLATE I

Fig. 1. Working the sampler on R.V. *Sabella*. The instrument is being hauled up. Note that cable has unwound from the drum so that the key has passed over the sheave. The safety rope may be seen on the right of this cable. A toothed scoop is being tested; the type normally used is seen on the deck. Note the weights attached at either end of the frame.

Fig. 2. Photograph of the new sampler. The scoop may be seen under the frame. The two jars of sand together represent the volume of one sample.



likewise working on oysters (*Ostrea virginica*), determined the percentage retention of cells of *Chlorella*, *Nitzschia*, and *Euglena* in the gills. For *Chlorella* cells (about 5μ in diameter) the value obtained varied from 0 to 92%. Apparently the gills function more efficiently at smaller concentrations than at larger ones. *Nitzschia* and even *Euglena viridis* (about 60μ) were also found to pass through the gills, only 15–80% of *Euglena* cells being retained. In these experiments no correlation was found between the number of cells present in the water and the percentage removed. ZoBell & Landon (1937) stated that the gills of the California mussel retain bacteria very efficiently, although these authors do not mention directly the degree of retention. Therefore it seems possible that the pore sizes of the gills of *Mytilus* are smaller than those of oysters. However, the question arises whether the efficiency of the gills in retaining particles is always the same in one and the same animal. This is probably not so. Apart from possible changes in pore sizes of the gill filters arising from changed contraction of muscle fibres in the gill filaments, the animals seem to have other means of changing the efficiency of the gills. MacGinitie (1941) observed the gills through glass windows in the shells and he found that lamellibranchs, when quite undisturbed, can produce a layer of mucus covering the gill surfaces. This sheet of mucus most probably retains particulate matter present in the water down to very small particles, in any case far below bacterial sizes. The mucus including the particles is transported towards the mouth opening by means of the cilia and ingested. MacGinitie holds the view that lamellibranchs are feeding, i.e. ingesting the collected food material, only when they are producing the sheet of mucus. Furthermore, he states that they will only secrete the mucus layer when they are quite undisturbed and have been so for some time, and only if they accept particulate matter in the water as food. According to this view, perhaps all earlier experiments on feeding rates of lamellibranchs are open to criticism in the sense that under the experimental conditions the animals have not really been feeding. Against this assumption it may be said that in many of the experiments mentioned an uptake of particles in the alimentary tract has actually been demonstrated. The possibility thus exists that lamellibranchs may feed both with and without formation of a mucus layer. It was therefore thought worth while to investigate further the feeding behaviour of the lamellibranchs under conditions as natural as possible, using suspensions of both 'natural' (micro-organisms) and 'artificial' (graphite) particles as medium.

Since the $\text{NH}_2\text{-N}$ content of an animal is a more satisfactory measure of the amount of living tissue than are length or weight, the feeding rate has been expressed per $\text{NH}_2\text{-N}$ unit in the experimental animals.

The experimental part of the present investigation has been performed at the Plymouth Laboratory. I wish to express my sincere thanks to the Director,

Mr F. S. Russell, for the great interest he has taken in the work and for providing all the necessary working facilities. My most cordial thanks are due to Dr Mary Parke who prepared the gallons of culture used. I am greatly indebted to Dr W. R. G. Atkins who suggested the use of the colloidal graphite, and to E. G. Acheson Ltd., London, who placed the graphite at my disposal. The work has been made possible through a grant from the Rask-Ørsted Foundation.

TECHNIQUE

Since small mussels seem to be less sensitive to handling and to changes in environment than larger individuals, the experiments were performed on small specimens of *Mytilus edulis* (L.) varying in length from about 1 to 5 cm. The mussels were collected from the piles of the old Plymouth pier. They were found to be most active when they remained in the naturally occurring clusters. To make sure that mussels of approximately the same size were used in the single experiments, the average size of the animals in the individual cluster was given preference, and animals of extreme sizes were removed together with those completely covered by their neighbours. Moreover, only those animals were chosen which were oriented so that their siphons were freely exposed to the surrounding medium. The resulting clusters contained between fifteen and fifty individuals, depending on the size of the individuals. The experimental vessels were of such shape and size that the mussels were able to keep the total water volume well mixed. Prior to the experiments, the mussels were adapted for several days to the running water from the circulation system of the laboratory. During that period the animals arranged themselves in an almost globular mass and moreover attached themselves to the bottom of the vessel by means of byssus threads. At the start of an experiment the water was replaced by the desired suspension, either freshly neutralized alga culture in vigorous growth diluted with tank water, or suspensions of graphite. A dilution of one part of alga culture with two to four parts of tank water was mostly used. Between subsequent experiments the animals were kept in running water. The temperature during the experiments varied between 17 and 20° C. The rate of feeding was computed from the formula

$$P_t = P_0 \exp \left[-\frac{m}{M} t \right],$$

where M is the quantity of water used for the experiment, and m the quantity 'cleared' from particles per unit time, while P_t and P_0 are the concentrations of the suspended material at the time t and 0, respectively (Jørgensen, 1943).

As suspended material *Nitzschia closterium* forma *minutissima*, and flagellates 'B', 'I' and 'J', which were kept in permanent culture in the Plymouth Laboratory, were employed. The first two of these have now been described by Parke (1949) and named *Dicrateria inornata* and *Isochrysis galbana*

respectively. Colloidal graphite was also used, from two different samples, viz. 'Prodag', grade 'C', and 'Aquadag', grade 'S', both supplied by E. G. Acheson Ltd., London. They are here referred to as graphite 'C' and graphite 'S'. The concentrations of the suspensions were determined photometrically by means of a portable 'Eel' photometer. $\text{NH}_2\text{-N}$ determinations were made according to Parnas' (1938) micro-modification of the Kjeldahl analysis.

RESULTS

The results obtained on the feeding behaviour of *Mytilus* differed according to the kind of suspensions used. The experiments with suspensions of graphite, flagellates, and *Nitzschia*, respectively, will be dealt with separately.

Experiments with graphite suspensions. When suspensions of graphite were used the values of the feeding rates decreased during the experiments. Some typical examples are given for graphite 'S' in Fig. 1, and for graphite 'C' in Fig. 2. Tables I and II summarize the numerical material obtained in experiments with graphite suspensions. Only the first and last values of feeding rates measured during one single experiment are recorded in the Tables (columns (iii) and (iv)). In column (v) the end value is expressed as a percentage of the value at the start. It is seen that at the time the experiments were concluded the feeding rates were often less than 10% of the feeding rates at the start. Sometimes, however, the decrease in feeding rate was only slight.

Two different mechanisms may be responsible for a decrease in feeding rate, viz. either a decreasing rate of transport of water through the gills, or a decrease in the percentage of suspended particles retained by the gills. Alternatively, both processes might occur simultaneously. Probably both mechanisms are of importance, as will appear from the following considerations.

During the experiments the general behaviour of the experimental animals was also studied. From observing the positions of the valves, the degree of extension of the siphons, and especially the movements on the surface of the water caused by the water currents produced by the animals, a rather rough measure for changes of the amount of water transported through the animals could be obtained. It was found that when the mussels were transferred from pure sea water to graphite suspensions they sometimes showed decreasing activity in the course of the experiment. This occurred in five out of seventeen experiments. In the twelve other experiments, however, there was no visible change in the activity of the mussels throughout the experimental period. Nevertheless, even under such circumstances the feeding rates were often much lower at the end of the experiment than at the start. Figs. 1 and 2 show two such examples; the same may be seen also from Tables I and II, column (vi), where notes have been made on such activity of the mussels as could be directly observed. In these mussels the percentage of particles retained by the gills decreased during the experiments.

The particles in the graphite suspensions were not all of equal size, as the

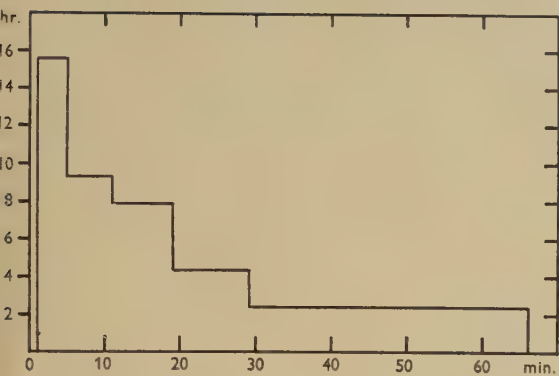


Fig. 1. Feeding rates in l./hr. of *Mytilus edulis* in suspensions of graphite 'S'.

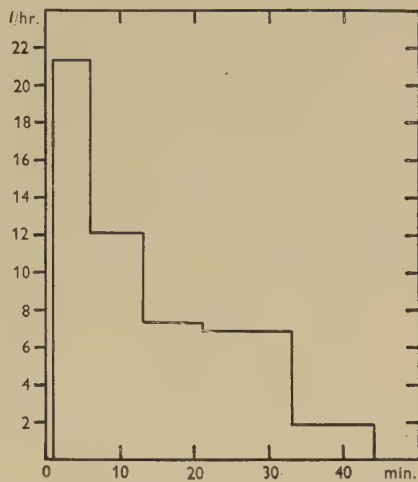


Fig. 2. Feeding rates in l./hr. of *Mytilus edulis* in suspensions of graphite 'C'.

TABLE I. EXPERIMENTS WITH SUSPENSIONS OF GRAPHITE 'S'

c means that the activity of the animals remained high and unchanged during the experiment, whereas *d* indicates that a decreasing activity was observed.

<i>Mytilus</i> (specimen no.)	Date	Feeding rate (l./hr.)		End value as percentage of initial value	
		Initial value	End value		
(i)	(ii)	(iii)	(iv)	(v)	(vi)
11	17. vi.	9.4	0.9	10	—
14	21. vi.	3.7	1.6	43	<i>c</i>
14	21. vi.	4.2	0.4	10	<i>d</i>
14	23. vi.	8.4	3.6	43	<i>c</i>
14	23. vi.	9.4	4.7	50	<i>c</i>
16	30. vi.	28.7	16.5	58	<i>c</i>
16	1. vii.	5.1	0.9	18	<i>c</i>
16	1. vii.	7.6	1.9	25	<i>c</i>
16	3. vii.	22.6	19.0	84	<i>c</i>
16	3. vii.	11.2	1.7	15	<i>d</i>
16	3. vii.	15.6	2.7	15	<i>c</i>
16	6. vii.	6.4	0.4	6	<i>c</i>
16	8. vii.	12.5	1.0	8	—

TABLE II. EXPERIMENTS WITH SUSPENSIONS OF GRAPHITE 'C'

<i>Mytilus</i> (specimen no.)	Date	Feeding rate (l./hr.)		End value as percentage of initial value	
		Initial value	End value		
(i)	(ii)	(iii)	(iv)	(v)	(vi)
11	17. vi.	5.8	1.8	31	<i>d</i>
11	18. vi.	13.1	2.4	18	—
11	18. vi.	9.4	2.2	21	—
11	18. vi.	21.3	1.9	9	<i>c</i>
16	3. vii.	26.2	24.5	94	<i>c</i>
16	3. vii.	33.5	31.0	93	<i>c</i>
16	7. vii.	6.5	2.5	38	<i>d</i>
16	8. vii.	12.5	1.0	8	<i>d</i>

graphite did not form totally dispersed and quite stable suspensions in sea water.¹ It is therefore natural to assume that the heterogeneity as regards particle size of the suspended material may be responsible for the decreasing feeding rates observed, the larger particles being more selectively retained by the gills. The average size of the basic particle in graphite 'S' suspensions was about 2μ and in graphite 'C' $4-5\mu$. The sizes of the aggregates of basic particles observed when the suspensions were examined under the microscope have not been measured. In order to investigate more closely the influence of particle size, the following experiments were made. In each of four

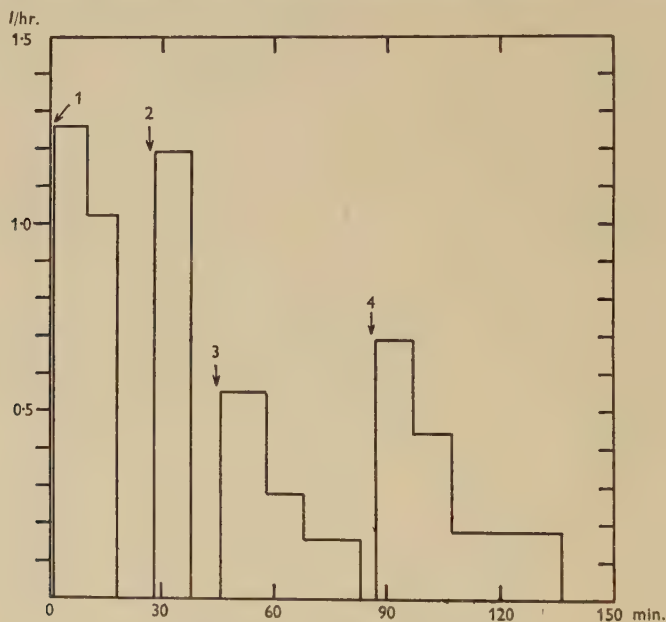


Fig. 3. For explanation, see text.

finger bowls were placed two mussels about 3 cm. in length. At the start of the experiment 250 ml. of graphite suspension were added to each of the bowls and the experiments were run until the concentration of the suspensions in each was reduced to about one-third. During this period, two determinations on the feeding rates were made. The second determination was always lower than the first. This is seen in Fig. 3, which represents the average

¹ A curve representing measurements of the light absorption (ampèremeter readings) at different dilutions of a standard suspension was used to determine the concentration of the suspensions during the experiments. Strictly speaking, this method is of course not admissible where the ratio between larger and smaller particles changes during an experiment, as most certainly occurred in the graphite experiments. With decreasing average particle size the densities of particles measured from the curve will be lower than the real densities, which means that the amount of water measured as cleared from particles will be too large. In fact, the decreases in feeding rates have been still larger than stated in the tables. This error will, however, not effect the conclusions to be drawn from the experiments.

of the four experiments. At the end of the period the suspension was decanted and stored for later use, and replaced by fresh graphite suspension taken from the same standard suspension as used previously. This time one determination of the feeding rate was made at the time when the concentration of the suspension was reduced to about one-half. Immediately after, the rest of the suspension was decanted and replaced by the suspension used initially. The feeding rates after the second addition of fresh suspension were always higher than the preceding ones. During the third period of the experiment the animals once more filtered the suspensions in which they had started until the concentration of the suspensions was about one-eighth of the initial value. It is seen that the values of the feeding rates decrease with time, and even at the start are lower than the preceding figures in fresh graphite suspension. Finally, the suspension left from the second period of the experiment was used once more. Immediately after addition of the suspension the feeding rates are relatively high, but they decrease later. This experiment, further, gives strong evidence for the view that under the prevailing experimental conditions *Mytilus* retained larger particles more efficiently than smaller ones.

Experiments with suspensions of flagellates. Of the three flagellates used in the experiments, *Dicrateria inornata* ('B') is spheroidal, about $3\text{--}5\cdot5\mu$ in diameter; *Isochrysis galbana* ('I') is ellipsoidal, $5\text{--}6\mu$ long, $3\text{--}4\mu$ broad and $2\cdot5\text{--}3\mu$ thick; whereas flagellate 'J' is ovoid, about $6\text{--}8\mu$ long and $3\text{--}4\mu$ broad. The results of the experiments are given in Table III. When using suspensions

TABLE III. EXPERIMENTS WITH SUSPENSIONS OF DIFFERENT FLAGELLATES

Mytilus (specimen no.)	Date	Feeding rate (l./hr.)		End value as percentage of initial value	
		Initial value	End value		
		(iii)	(iv)	(v)	(vi)
		Flagellate 'J'			
2	13. vi.	1.0	0.11	11	—
8	13. vi.	0.21	0.44	209	—
9	13. vi.	0.23	0.29	126	—
11	19. vi.	6.6	14.5	219	—
11	19. vi.	29.5	29.0	98	—
11	19. vi.	29.5	29.5	100	—
<i>Isochrysis galbana</i>					
14	23. vi.	3.3	5.4	163	—
14	23. vi.	3.4	2.8	82	—
16	30. vi.	9.0	10.1	112	—
16	30. vi.	7.2	9.7	135	—
16	6. vii.	11.4	21.3	187	—
<i>Dicrateria inornata</i>					
2	14. vi.	0.28	0.26	93	—
8	14. vi.	0.38	0.10	26	—
9	14. vi.	0.17	0.17	100	—
11	19. vi.	19.4	3.5	18	—
11	19. vi.	28.0	1.1	4	c
14	23. vi.	10.0	4.4	44	c
16	26. vi.	13.5	15.0	111	—

of the two last, the feeding rates measured were usually constant or increasing during the experiment. Only in one experiment out of eleven a pronounced decrease was observed. With *Dicrateria*, four experiments out of seven showed a pronounced decrease in feeding rates with time. In some of these at least the transport of water through the animals did not change noticeably, as judged from the direct observations of the behaviour of the mussels and the movements of the water. The decreasing feeding rates must therefore be caused by a decreasing retention of flagellates in the gills. As the particle size of the suspension is rather uniform, this factor cannot explain the decreasing rate. It seems that the 'pore' sizes of the gills can be changed so that the gill filter may be more or less permeable to particles of the same size. Furthermore, a comparison of Tables I, II and III shows that when suspensions of flagellates are used the feeding rates obtained are usually much higher than the feeding rates found with graphite suspensions in the later parts of the experiments when the smaller particle sizes most certainly dominate. This holds especially when the flagellate 'J' experiments are compared with the graphite experiments. See, for example, the experiments on *Mytilus* specimen no. 11 from 17 to 18 June (graphite) and from 19 June (flagellate 'J'). This means that the gills of the mussels may, and normally do, retain flagellates much more effectively than graphite particles even when these two kinds of particles are of about the same size.

Experiments with Nitzschia. The experiments with suspensions of *Nitzschia* lead to rather uniform results (Table IV). The feeding rates were found to be

TABLE IV. EXPERIMENTS WITH SUSPENSIONS OF *NITZSCHIA*

<i>Mytilus</i> (specimen no.)	Date	Feeding rate (l./hr.)		End value as percentage of initial value	
		Initial value	End value		
(i)	(ii)	(iii)	(iv)	(v)	(vi)
11	18. vi.	6.2	11.9	192	—
14	21. vi.	6.0	7.8	130	—
16	26. vi.	15.0	19.0	127	—
16	27. vi.	9.5	13.2	125	—
16	27. vi.	13.4	13.7	102	—
16	30. vi.	10.4	13.5	130	—
16	30. vi.	10.4	14.3	137	—
16	1. vii.	28.0	29.0	103	—
16	3. vii.	12.7	21.6	170	—
16	3. vii.	19.1	25.1	131	—
16	3. vii.	27.5	28.4	103	—
16	5. vii.	12.0	20.3	169	—
16	5. vii.	17.2	23.9	139	—
16	5. vii.	21.2	20.4	96	—
16	5. vii.	19.4	9.0	46	<i>d</i>
16	7. vii.	8.5	10.8	127	—
16	8. vii.	5.3	10.9	206	—

constant or, most often, to increase during the experiments. Only in one experiment out of seventeen was there observed a pronounced decrease in the

rate of feeding, when it was very conspicuous that the water propulsion from the mussels had also diminished towards the end of the experiment. The pronounced tendency to lower feeding rates, which was found at the start of the experiments with *Nitzschia* as well as in many of the experiments with flagellate 'J', is most probably caused by the heavy load of micro-organisms deposited on the gills at the start of the experiments. The suspensions used were comparatively thick, as could be estimated from the large amounts of pseudo-faeces formed by the mussels.

DISCUSSION

The results from the experiments on the feeding rate of *Mytilus* in different suspensions seem rather divergent. In graphite suspensions containing particles ranging from about 2μ and $4-5\mu$ to much larger ones, the larger particles were most frequently found to be retained more effectively than the smaller ones. Occasionally, however, the feeding rates were found to be high and almost constant during the experiments, thus indicating that the percentage of graphite particles retained by the gills had been high and independent of particle size (e.g., Table II, specimen no. 16, 3 July). In suspensions of flagellates with an average particle size close to the minimum size of particles in suspensions of graphite 'C', the percentage of micro-organisms retained by the gills was usually high and remained constant during the experiment, but in some instances it decreased. Once, indeed, the last measured feeding rate was only 4% of the feeding rate found in the beginning of the experiment (Table III, specimen no. 11, 19 June). In the later periods of the graphite experiments, when most of the bigger particles had presumably been removed from the suspension, the feeding rates were often found to be less than 10% of the feeding rates in suspensions of flagellates. This was observed even when there was no indication of a lower rate of water transport through the experimental animals. It must therefore be concluded that, under certain conditions, the gills of *M. edulis* retain only a small fraction of particles about 5μ in diameter, whereas, at other times and under different conditions, particles of the same size are retained much more efficiently. This observation concerning the ability of the gills is in good agreement with the investigations of MacGinitie (1941) on the feeding behaviour of lamellibranchs referred to on p. 334. If MacGinitie's observations are taken into account the present experiments may be interpreted in the following way. In graphite suspensions *Mytilus* must be assumed normally not to accept the particles as food. Consequently they will not produce a mucus cover on the gills, and the efficiency with which particles are retained will depend entirely upon the particle size. That the mussels were genuinely disturbed in graphite suspensions could be seen from the fact that in five out of seventeen experiments with graphite decreasing activity during the experiments manifested itself in the general behaviour of the animals. On the other

hand, presentation of flagellate suspensions to the mussels clearly as a rule had no depressing effect on the formation of the mucus layer. In this event the retention of micro-organisms by the gills must have been approximately complete. It is difficult to imagine how flagellates should be able to penetrate a layer of mucus. In the experiments with *Nitzschia* it must be assumed, too, that the retention of cells in the gills was almost complete, as the feeding rates found were of the same order of magnitude as in the flagellate experiments. Moreover, only in four experiments out of twenty-nine with suspensions of flagellates or *Nitzschia* was decreasing activity of the mussels, with respect to the transport of water, observed during the experiments. This also indicates that the mussels tolerated and accepted the suspended material.

From the above considerations it must be assumed that the constant feeding rates found in suspensions of flagellates and *Nitzschia* probably give the total volume of water transported through the gills. Table V collates the values of

TABLE V

Mytilus (specimen no.)	Date	Average length (cm.)	No. of animals	NH ₂ -N (mg.)		Suspension	Feeding rate in ml. per hr. per mg. N
				Total	Average per animal		
14	21. vi.	1.5	56	110	2	<i>Nitzschia</i>	63
14	23. vi.	1.5	56	110	2	<i>Dicrateria</i>	94
14	23. vi.	1.5	56	110	2	<i>Isochrysis</i>	81
14	23. vi.	1.5	56	110	2	<i>Dicrateria</i>	86
14	23. vi.	1.5	56	110	2	<i>Dicrateria</i>	74
Average							80
16	26. vi.	2.9	25	555	22	<i>Nitzschia</i>	31
16	27. vi.	2.9	25	555	22	<i>Nitzschia</i>	24
16	30. vi.	2.9	25	555	22	<i>Isochrysis</i>	16
16	30. vi.	2.9	25	555	22	<i>Nitzschia</i>	22
16	30. vi.	2.9	25	555	22	<i>Nitzschia</i>	23
16	1. vii.	2.9	25	555	22	<i>Nitzschia</i>	51
16	3. vii.	2.9	25	555	22	<i>Nitzschia</i>	37
16	3. vii.	2.9	25	555	22	<i>Nitzschia</i>	47
16	5. vii.	2.9	25	555	22	<i>Nitzschia</i>	37
11	19. vi.	3.2	24	657	27	Flagellate 'J'	23
11	19. vi.	3.2	24	657	27	Flagellate 'J'	44
11	19. vi.	3.2	24	657	27	Flagellate 'J'	45
11	19. vi.	3.2	24	657	27	<i>Isochrysis</i>	48
Average							34

the feeding rate (=water transport) from experiments with flagellates and *Nitzschia*. All experiments performed are included in it, except for those in which the mussels were not fully open and active during the experimental period. The feeding rates are shown to be comparatively larger in the smaller animals than in the bigger ones. *Mytilus* containing about 2 mg. NH₂-N per animal filtered about 80 ml. water per hr. per mg. NH₂-N, whereas the value was about 30-40 ml. for animals containing about 20-30 mg. NH₂-N.

In order to compute the diurnal feeding rate from these values it is necessary to know the ratio between rest and activity in the course of 24 hr. Loosanoff (1942) found that, within a wide range of temperature, *Mytilus edulis* is most probably almost constantly active. Between 5° and 18° C. the valves were open throughout 97–99% of the time, and food was always found in the stomach. It therefore seems justified to consider *Mytilus* feeding almost permanently when undisturbed. This behaviour may apply generally to plankton-feeding lamellibranchs (Loosanoff, 1939; Loosanoff & Nomeiko, 1946).

MacGinitie (1941) states that lamellibranchs normally ingest food only when they are forming the sheet of mucus on the gills. If the mucus layer is not being formed particles collected on the gills and transported by the ciliary mechanisms to the labial palps will be rejected there without entering the mouth. These statements are in disagreement with the observations made in the present investigations. In the graphite experiments, the mussels frequently could not have secreted a sheet of mucus, as they were unable to retain the smaller graphite particles. Nevertheless, they were very often found to be ingesting all the graphite which had been retained by the gills. Formation of pseudo-faeces did not necessarily occur, but, *c.* 30–60 min. after the addition of the graphite suspension, large amounts of real faeces were rejected through the exhalant siphon. Several examples may also be found in the literature describing ingestion of food without formation of the 'feeding mucus'. Loosanoff & Engle (1947), for example, observed formation of large quantities of true faeces in *Ostrea virginica* fed on suspensions of *Chlorella* which were only partly retained by the gills. When feeding proceeds by means of the mucus sheet on the surface of the gills, no selection according to particle size is possible of particles imbedded in the mucus. On the other hand, we know, for instance through the very accurate and comprehensive work of Atkins (1936–38), that the gill surface possesses a very elaborate pattern of cilia which are able to sort and transport particles according to size for the purpose of either rejection or ingestion. It is difficult to believe that this complicated system of cilia should have nothing whatsoever to do with the normal feeding mechanisms of the lamellibranchs. Therefore it may be necessary to include in the normal feeding behaviour of lamellibranchs feeding *ad modum* MacGinitie as well as feeding by means of the filtering and sorting mechanisms provided by the cilia of the gills.

SUMMARY

The feeding rate of small specimens of *Mytilus edulis* (L.) has been determined in suspensions of colloidal graphite ('Prodag', grade 'C', and 'Aquadag', grade 'S'), of flagellates, and of *Nitzschia closterium*. The feeding rate was measured as the volume of water cleared from particles per unit time. In graphite suspensions, with particle size of about 4–5 μ , as a rule only a small

percentage of the particles was retained by the gills, whereas flagellates of about the same size were normally nearly all retained. This difference in behaviour of the animals when kept in suspensions of graphite and flagellates, respectively, is discussed in the light of MacGinitie's observations. This author found that lamellibranchs, when feeding, secrete a continuous layer of mucus on the gills which are then able to retain even very small particles suspended in the water. When the animals are disturbed, or dislike the 'food', the formation of 'feeding mucus' is interrupted and small particles may pass and escape between the gill filaments. Therefore, it can be assumed that the mussels, when transferred to graphite suspensions, will stop forming the mucus sheet, with the result that only a small fraction of the $4-5\mu$ graphite particles are retained by the gills. On the other hand, the layer of mucus is secreted in suspensions of flagellates, which consequently are retained in bulk by the gills. Complete retention was normally also observed in suspensions of *Nitzschia*. The feeding rate in suspensions of flagellates and *Nitzschia* was found to be c. 80 ml. per hr. per mg. $\text{NH}_2\text{-N}$ in mussels containing about 2 mg. $\text{NH}_2\text{-N}$ per animal, and about 30-40 ml. in mussels containing about 20 mg. $\text{NH}_2\text{-N}$.

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NOTES FROM THE PLYMOUTH AQUARIUM

By Douglas P. Wilson, D.Sc., F.R.P.S.

Zoologist at the Plymouth Laboratory

(Plate I)

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During the daily maintenance work of a large aquarium many casual observations are made on the habits of the inmates. These are sometimes worthy of record, though too slight in themselves to justify separate papers each under its own distinctive title. It has, however, been thought fit to bring together in the form of a series of notes some of the more interesting of these observations. It is not intended to discuss each with full reference to the comparable literature; rather are they presented as raw material for the use of other investigators in their own specialized fields. Most of these observations have been made since the re-establishment of the Plymouth aquarium in 1946 (after its war damage), and up to the date of writing, November 1948.

A DISEASE OF *ADAMSIA PALLIATA* (BOHADSCH)

In a shallow table tank strewn with shell-gravel there are regularly displayed a varying number of small hermit-crabs, *Eupagurus prideauxi* (Leach), with their cloak anemones, *Adamsia palliata* (Bohadsch). Normally the hermit-crabs die before the anemones, necessitating the removal from time to time of an accumulation of the latter from the bottom of the tank. It was therefore an unprecedented happening when on 17 March 1947 all the cloak anemones were found to be dead or almost dead, with most of the colour gone and the soft tissues shrunk away from their cuticular bases. Many had dropped off altogether to lie decaying on the gravel. The hermit-crabs themselves were alive and well but they looked peculiarly naked, their abdomens covered only with the thin brown cuticles of their late companions and the now absurdly small gastropod shells of their earlier youth.

Whatever it was that had killed the anemones had acted quickly. Two days before it had been noticed that the anemones were sickly, though previously there had been nothing unusual about their appearance, the tank having been looked over daily. About half the hermit-crabs and anemones present had come in straight from the sea less than a week before the catastrophe; others had been in the aquarium much longer, some perhaps for several weeks. The disease was probably introduced with the latest arrivals. There was no evidence of protozoan or other obvious parasites. (I am indebted to Mr Y. R. Tripathi for assisting me in the search for parasites.) The disease may therefore have been caused by some extremely small micro-organism.

On 20 March six hermit-crabs with cloak anemones newly brought in from the sea were put into the tank. Four days later the anemones were very ill and had begun to shrink away from their cuticular bases. On the next day their columns showed ugly lesions, and on the following day they were even worse, being almost detached from the basal cuticle. On this day (27 March) the tank was cleared of all hermit-crabs, anemones and visible traces of them and a new lot, procured by trawling, put in. In a few days these too had the disease and further batches also caught it soon after arrival. All this time there were a few hermit-crabs and anemones of the same species in another tank elsewhere in the building and these continued to be healthy, although the water running into their tank was supplied by the reservoir into which water from the diseased tank was draining.

On 2 May the entire contents of the diseased tank were removed and got rid of. The tank was emptied and swilled with antiseptic (Dettol) for 20 min. The antiseptic was washed away and the tank swabbed dry. It was then reflooded with sea water, new and well-washed shell gravel was strewn over the bottom, and a new lot of hermit-crabs with cloak anemones were put in. These had been caught a few days previously and acclimatized in another tank. There was no further trouble and there has been no recurrence of the disease.

LONGEVITY OF SABELLIDS

Many animals, once they have become accustomed to life in an aquarium, survive for many years. This is especially true of hardy fishes like grey mullet and bass for which a period of twelve or fifteen years in one tank is nothing unusual. Some invertebrates also reach and may exceed these figures (e.g. some sea-anemones) but only rarely are individual invertebrates kept sufficiently well isolated from others of their kind for definite records to be established.

In a tank containing grey mullet there had been for at least several months before the war one solitary *Sabella pavonina* Savigny var. *bicornata* Hornell (Ewer, 1946). This particular tank was one of the few to escape serious damage by enemy action, and throughout the war this sabellid maintained its position in the bottom gravel close to one side—and it is still there. The tank was emptied

and cleaned in 1946, but the worm was saved and replaced in its old position. It has therefore been alive for at least 10 years and during that period it has not been known to renew its crown, though this may have happened during periods when I have been away from the Laboratory.

In the same tank, close to the *Sabella*, is a piece of limestone dredged from the Sound; it also has been in the tank since before the war. It was selected for exhibition because of the large number of the boring sabellid *Potamilla torelli* Malmgren which it contained. To-day there are fewer of these worms to be seen than there were originally, but the stone is still a beautiful sight when all have expanded their crowns. It is not known whether the worms still living were present in the stone when it was dredged ten years or so ago, or whether they are newcomers. Some may be newcomers, for it is known that sabellids can breed in the aquarium system. Lately several *Branchiomma vesiculosum* (Montagu) have appeared in several tanks, particularly those with sandy bottoms, which had never had any of these worms put into them. The species is kept in other tanks in the same circulatory system, and the free-swimming larvae must have been carried round through the pump.

AN APPARENT EXAMPLE OF LEARNING IN *PALINURUS VULGARIS* LATREILLE

In 1947 there were together in a large tank four or five *Palinurus vulgaris* Latreille and twenty or more large hermit-crabs, *Eupagurus bernhardus* (L.), in whelk shells on which were usually one or more parasitic anemones, *Calliactis parasitica* (Couch). The only other inhabitants of the tank were a few flounders. For some months these lived together peacefully and then, at a time when food was scarce, the *Palinurus* attacked the hermit-crabs, pulled them out of their shells and ate the soft abdomens. They continued this habit even when well fed. Any new hermit-crabs put into this tank were soon found and eaten and it was no longer possible to keep hermit-crabs with these particular rock lobsters. The latter were therefore removed and replaced by a similar number from another tank. The new *Palinurus* did not attack the hermit-crabs though kept with them for several months, and though they too sometimes went short of food during periods of scarcity.

REGENERATION OF ARMS IN *MARTHASTERIAS GLACIALIS* (L.)

In May 1947 a specimen of *Marthasterias glacialis* (L.) regenerating four arms was brought in from the sea. The four regenerating arms were relatively short, about 2 cm. long, the fifth and unregenerated arm being about 15 cm. in length. This starfish was photographed shortly after arrival and was then kept in a small tank apart from any others of the same species. From time to time it was fed on mussels or on pieces of squid, but feeding was irregular and there were often long periods without food. The four regenerating arms slowly increased in size but they were still only a fraction of the length of the fifth arm when in

July 1948 the latter broke off at the disk and died. It may be that irregular and insufficient feeding had brought about some wastage of tissues, perhaps to supply materials to the regenerating arms. However that may be, there was soon to be seen on the side of the disk at the place where the old arm had been severed the rudiment of a new one. Now, in November 1948, the starfish consists of a disk about 2 cm. in diameter, four arms 6–7 cm. long and one arm 1.5 cm. long. There is some difference in appearance between the tissues of various ages, especially as regards colour, the disk being darkest and the newest arm lightest in tone. Thus had the specimen come in from the sea in its present condition, careful examination would have revealed the history of these events. Presumably in time the colour differences between the tissues of three distinct ages will become less and when the arms reach sizes commensurate with the disk there will be produced a starfish showing little or no trace of its history. The age of such a starfish is the age of its disk. In the sea such accidents to the arms may well delay growth of the disk and result—when the new arms have grown to match the disk—in a starfish, apparently normal and complete, but considerably smaller than others of the same species and age living under identical feeding conditions.

REGENERATION OF FINS IN *TRIGLA HIRUNDO* BLOCH AND *MUGIL CHELO* CUVIER

There are comparatively few references in the literature to the regeneration of fins in fishes. Aquarium keepers know that in due course torn fins usually heal to show no signs of injury, but actual records are not numerous.

In the autumn of 1946, not long after the reconstruction and reopening of the aquarium, a sapphirine gurnard, *Trigla hirundo* Bloch, about a foot long, was brought in from the sea and put into a tank with some others. It had been damaged in the trawl and for several days was very ill. Almost the whole of the upper lobe of the caudal fin showed extensive bruising and before long the tissues died and rotted away. The 'fingers' of both pectoral fins were likewise bruised, and similarly rotted away for about half their lengths. The condition of the fish was such that it was expected to die and there was some intention of removing it from the tank before it did so. However, some signs of recovery were noticed and it was allowed to remain, although for several weeks supuration of the fingers was marked and the lesion of the caudal fin was inflamed. Slowly the wounds healed and eventually it was seen that the upper lobe of the caudal fin was being regenerated. For several months this regenerating lobe was darker in colour than the lower and it was, of course, much smaller. By the end of the first year it had by no means reached the dimensions of the lower lobe and even now, two years after the event, the upper lobe is still a little smaller than the lower. The fingers were also regenerated, some of them abnormally, the new growths being directed ventrally at various angles to the

old proximal parts. On the third finger of the left pectoral the angle is so acute that this particular finger is bent right back on itself. Some of the less acutely bent fingers are now straightening out.

In mid-June 1947 thirty or forty medium-sized grey mullet (*Mugil chelo* Cuvier) were caught in a seine-net in the estuary of the River Yealm and transported to a large reserve tank outside the main aquarium building. Within two or three days all the fish showed extensive bruises and each one had a mark around the head, or forepart of the body, where a mesh of the net had encircled it. Almost all the fins were torn and lacerated, particularly the caudal and paired fins which were extensively frayed with bared fin rays; in some instances only the stumps of the pectorals were left. Some of the fish died but more than half survived, their lesions becoming covered with thick brown scabs, often extensive, on head and body. In this condition they remained for several weeks, eventually feeding well. Towards the end of July and during August the scabs were reduced and disappeared entirely. At the same time the fins were regenerated and by September the fish were clean and fit for exhibition. Two or three of them were put with the grey mullet we have had for many years but most of them were sent by rail to the London Zoo aquarium where they are still living. The few kept in Plymouth still show marks, apparently scabless, where the deeper bruises had been.

PARTIAL BURYING OF *TRIGLA HIRUNDO* BLOCH

Before the war *Trigla hirundo* Bloch were kept in a tank strewn with small pebbles; they are now kept on a sandy bottom and this has led to the observation that they can bury themselves, at least partially (Pl. I). The burying habit was most noticeable during the winter of 1947-48, especially did it take place late in the evening after the aquarium had been in darkness for a few hours. Burying has also been noticed during the daytime, particularly in the autumn of 1948 when the temperature of the water was falling rapidly. The observations are insufficient to associate the habit with low or falling temperatures, or with low light intensity, but they do at least indicate that it is usual for these fishes partially to bury themselves in the sea-bottom from time to time. The closely allied sea robins (*Prionotus*) are stated to bury themselves up to the eyes when disturbed (Romer, 1941).

The sand in the tank is not very deep and it seems likely that the fish would have covered themselves more completely had they been able to do so. The closed caudal fin was sometimes completely buried and the sand was heaped up on each side of the body towards the lateral line. Except for the fingers the pectoral fins were out of sight under the sand; the fingers emerged from it and were visible. The head was never covered in any way and the gill-slits were free from sand, respiration taking place in the usual manner and being unimpeded.

SHOALING OF *Gobius flavescens* FABRICIUS

It has been the practice for some years to keep *Gobius flavescens* Fabricius in the largest tank in the aquarium, together with conger eels, dogfishes, nurse-hounds and large turbot. They swim about in the tank and are but little inclined to rest on the bottom or on the rocks, their habit being pelagic rather than demersal. The larger fishes take no notice of them, presumably because they are too small to tempt their appetites. The gobies normally swim about individually with no tendency to shoal. They progress with jerky forward motions produced by the beating of the pectoral fins, their chief organs of locomotion.

In the summer of 1948 two or three hundred young fishes of this species, each an inch or less long, were netted in shore pools and placed in the tank. Instead of dispersing immediately they kept together in compact rather globular shoals, each consisting of fifty or a hundred fishes. For one or two days these shoals moved slowly through the tank keeping more or less in mid-water. The jerky forward motions of the fishes were out of step and gave a curious scintillating appearance to the shoals. Gradually the shoals became less compact and in a few days each little fish was swimming about its business without reference to its neighbours. The gobies scattered throughout the tank, mainly in the lower levels but a few swam well up near the surface. Since then there has been no tendency to shoal, although occasionally the fishes gather into straggling groups. Perhaps the shoaling was a fear reaction induced by capture and by strange surroundings; perhaps it takes place in the sea when the gobies are very young, or when alarmed.

BLENNIUS GATTORUGINE BLOCH GUARDING EGGS

Early in April 1946 a *Blennius gattorugine* Bloch spawned in a corner at the back of a medium-sized tank in the research laboratories. There was some sandy gravel on the bottom of the tank but no rockwork, and the eggs were attached in a single layer to the vertical slate. They were assiduously guarded by what was presumably the male parent, and his devotion continued for many weeks although the eggs soon died and therefore did not hatch. It was the end of June before he ceased to guard them. It would be of some interest to know whether the hatching of the eggs would have been a signal for the guarding fish to cease his duties and whether this long and fruitless devotion was due to the signal not having been given.

There were several other specimens of the same species in the tank, but at the time there seemed no doubt at all that it was the same fish on guard the whole time. Any other fish approaching the vicinity of the eggs was vigorously chased away.



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EXPLANATION OF PLATE I

Trigla hirundo Bloch, partially buried in sand, about 8.30 p.m. in December 1947. The tracks in the sand were produced by the lower lobe of the caudal fin dragging along the bottom as the fish walked on its 'fingers'. Photograph by flashlight.

SHORT-PERIOD FLUCTUATIONS IN THE NUMBERS OF BARNACLE LARVAE, WITH NOTES ON COMPARISONS BETWEEN PUMP AND NET PLANKTON HAULS

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(Text-figs. 1-7)

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INTRODUCTION

In the course of a series of daily plankton hauls, made over a period of over four years (Pyefinch, 1948), indications had been noted of variations in the numbers of barnacle larvae at different phases of the tide. It was also possible that diurnal variations occurred in the numbers of these larvae present near the water surface, and an attempt was therefore made to discover the extent of these variations.

It is clearly essential that an investigation of this character should be quantitative, and hauls were therefore made by pumping water through plankton nets. Hauls made by allowing plankton nets to fish from Keppel Pier during the ebb tide were, however, maintained throughout the period over which the pump hauls were made, so that comparisons could be made between the results obtained by the two methods.

Though the results of the investigation of the possible occurrence of tidal and diurnal variations in the numbers of barnacle larvae in the surface waters cannot be considered to be more than suggestive, the comparisons between pump and net hauls have revealed a number of points of interest, which it seems useful to place on record.

Acknowledgement is made to the Marine Corrosion Sub-Committee of the British Iron and Steel Research Association for their permission to publish

this work. Grateful acknowledgement is also due to the Scottish Marine Biological Association for the loan of the equipment used, and the author is especially indebted to Dr H. J. Thomas for his share in the labour of the serial hauls.

METHODS

Hauls were made using a Standard-Gwynne centrifugal pump, fitted with an armoured suction hose approximately $3\frac{1}{2}$ in. in external diameter; the delivery hose was also armoured and was approximately $2\frac{1}{4}$ in. in external diameter. A cylindrical copper rose was fitted to the suction hose; this rose was approximately 7 in. long and 4 in. in diameter (external dimensions) and was drilled with $\frac{3}{8}$ in. holes, $\frac{1}{2}$ in. between centres.

The suction hose hung over the seaward end of the landing stage of Keppel Pier and the water pumped was directed into a plankton net supported over a tank situated on the pier. The rose of the suction hose was adjusted to a constant depth before each haul was made. For the earlier hauls this was 3 ft. below the water surface, but for the later hauls (those made from 29 March onwards) the rose was adjusted to a depth of 2 ft. below the surface before each haul. This adjustment could only be made approximately, especially when heavy seas were breaking. Hauls made at various depths showed little variation in the numbers of larvae, over the range possible with this pump, so that it is unlikely that the alteration in depth of rose from 3 to 2 ft. mid-way through the series of readings described below caused any significant difference in the results obtained.

The capacity of the receiving tank was 350 l., but the volume of water filtered through the net was usually 333 l. (0.3 m^3). The volume of water which was pumped through the net was measured and the time taken to pump this volume of water was also recorded. This was done to ensure that approximately the same rate of pumping was maintained throughout, to minimize errors which might arise if gross variations in rate occurred. By adjustment of the water outlet valve and the throttle a reasonably uniform rate of pumping was achieved, of the order of 200 l./min. This is the minimum rate recommended by Wiborg (1948).

Most of the larvae collected were intact and so were readily identified, but there was evidence of some damage during passage through the pump, as isolated naupliar and cyprid appendages occurred occasionally in the hauls; these are rarely seen in hauls made by fishing a net from the pier. Larger planktonic forms (e.g. *Calanus*) were usually damaged, though it is not impossible to obtain samples of such larger forms using a pump, as Gibbons & Fraser (1937), using a different type of centrifugal pump, have obtained hauls of much larger planktonic forms than barnacle larvae in an undamaged state.

The site chosen for collecting these pump hauls was by no means ideal, but it was the best possible within reasonable working distance of the laboratory.

The chief disadvantage was that the rose was immersed very near to a barnacle-covered surface, so that there was a danger that larvae liberated from these barnacles could be taken directly into the suction hose; this seems likely to have occurred on at least one occasion during the sampling. On the other hand, the pump samples were taken as near as possible to the point from which plankton nets are usually fished, so that comparisons between the two types of haul could reasonably be made. It should be pointed out, however, that the currents flowing through the pier are undoubtedly complex, due to the obstruction of the piles, so that conditions cannot, in all probability, be regarded as strictly comparable. Any investigation of inshore planktonic forms seems bound to encounter difficulties of this nature, since hauls must be taken at sites where the hydrodynamic conditions are complex, due to the irregularities of the neighbouring shore.

SERIAL HAULS

Three sets of serial hauls, each extending over 24 hr. or longer, were made and these were supplemented by other series carried out over shorter periods. The first set of serial hauls was made on 11 and 12 March, the second set on 23 and 24 March, and the final set from 29 March to 1 April 1948.

Table I shows the average numbers of the larval stages of *Balanus balanoides*, *B. crenatus* and *Verruca stroemia* during these three periods, as averages for the 3-day period most closely corresponding to the period of the serial haul. These were obtained in hauls made from the pier in the usual way, by fishing a net for 1 hr. during the ebb tide. The first set of serial pump hauls was thus made during a period when early-stage nauplii predominated, the second set at a time when later-stage nauplii were more abundant, and the third set just when cyprids (particularly those of *Balanus balanoides*) were beginning to be plentiful.

TABLE I. AVERAGE NUMBERS OF BARNACLE LARVAE OCCURRING IN NET PLANKTON HAULS DURING THE PERIODS WHEN SERIAL PUMP HAULS WERE MADE

Period	Species	Average numbers of larvae present						Cyprid
		Nauplius						
		I	II	III	IV	V	VI	
10-12 March	<i>B. balanoides</i>	3845	20925	1460	260	40	0	0
	<i>B. crenatus</i>	565	4390	360	120	40	0	0
	<i>V. stroemia</i>	4320	5090	1075	600	20	0	0
22-24 March	<i>B. balanoides</i>	10	175	1065	3290	3235	4620	215
	<i>B. crenatus</i>	10	120	80	560	615	743	240
	<i>V. stroemia</i>	10	200	125	470	4120	35	0
29-31 March	<i>B. balanoides</i>	0	190	405	1745	1115	2895	9885
	<i>B. crenatus</i>	25	185	675	1705	1705	1490	205
	<i>V. stroemia</i>	5	20	35	415	4245	515	105

It was originally hoped that it would be possible to carry out further sets of serial hauls, but the numbers of larvae decreased so considerably after 9 April, that further series showed no promise of profitable results.

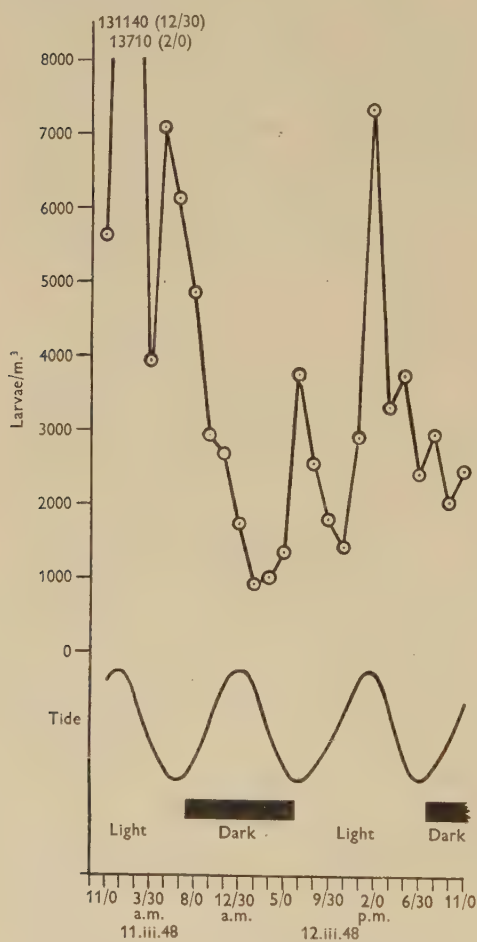


Fig. 1. Total barnacle larvae in the serial hauls of 11-12 March.

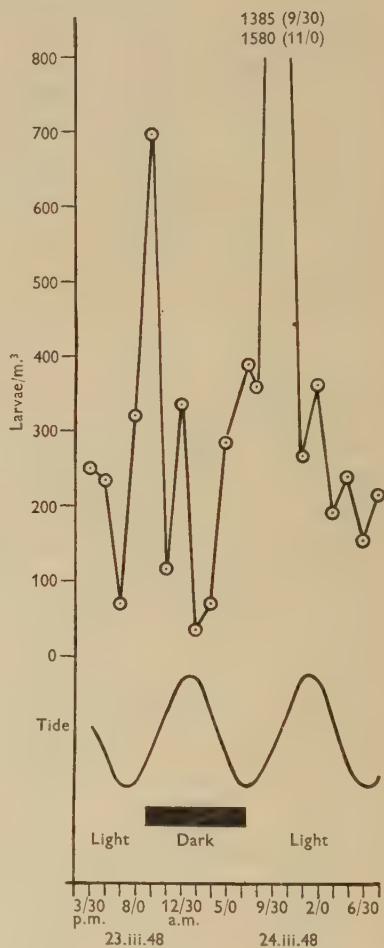


Fig. 2. Total barnacle larvae in the serial hauls of 23-24 March.

Series of 11-12 March. The results of this series are shown in Fig. 1. It would appear that the numbers of larvae present in the surface waters are reduced during the hours of darkness and, further, that maximum numbers of larvae are present at high water during the day, but not at high water during the night.

It will be noted that this graph is drawn for 'total nauplii', i.e. all stages present of the three species. A further analysis of these data suggests that the

generalizations just quoted are too clear cut. The exceptionally heavy haul taken at high water on 11 March consisted chiefly of the 1st-stage nauplius of *B. balanoides* (86% of the haul), whereas the maximum shown at high water the following day contained no 1st-stage nauplii of *B. balanoides*, but considerable numbers of the 2nd-stage nauplius, supplemented by 1st- and 2nd-stage nauplii of *B. crenatus*. It would seem reasonable to suggest that the maximum which occurred on 11 March was unusual; it may well have been produced by the liberation of nauplii from a small number of *B. balanoides* followed immediately by their uptake into the suction. Moore (1935) states that a single individual of *B. balanoides* can produce 13,000 nauplii, so that the product of only a few individuals would be needed to give the number of these larvae recorded in this haul.

Series of 23-24 March. The results of these hauls are shown in Fig. 2. The general outline of this curve is less regular than that shown in Fig. 1, fluctuations between successive hauls being more marked. This may well be due to the smaller numbers of larvae taken during this series, as it will be noted that the vertical scale of Fig. 2 is ten times that of Fig. 1.

Apart from the fact that the numbers of larvae taken during the hours of darkness were again rather smaller than those taken during the day, there is little correspondence between Figs. 1 and 2. In the present series there is no suggestion of a significant maximum at high water, the largest numbers of larvae being taken during the flood tide, both at night and during the day. The constitution of these two maximum hauls was similar, i.e. roughly the same proportion of the naupliar stages of each of the three species occurred in each haul. It is thus possible that, as this series of hauls was taken at a time when later-stage nauplii were abundant, this difference in behaviour is genuine and that the migrations of these stages differ from those of the earlier stages. In view, however, of the results obtained from the third series (see pp. 357-60) and of the considerable fluctuations that can occur in larval numbers over short periods of time (see p. 362), this suggestion does not seem likely to be correct.

Though cyprids (particularly those of *B. balanoides*) were obtained in these hauls, the records of their occurrence have been omitted from Fig. 2, as the numbers obtained were so small.

Series of 29 March-1 April. This series of hauls was made at the time when the cyprids of *B. balanoides* were beginning to become abundant; separate graphs have therefore been given of the total nauplii (Fig. 3) and the total cyprids (Fig. 5).

Fig. 3 presents a record which is even less regular than that of Figs. 1 and 2. The numbers of larvae present during the night were again rather lower than those present by day, but otherwise maxima seem to be irregular in their incidence. During the first night of the series a maximum occurred just after darkness had fallen, at the time of low water, whereas at the corresponding time 24 hr. later, naupliar numbers were practically at their minimum, but

there were signs of a maximum near the time of low water during the third night. During the day two maxima occurred at low water, two during the flood tide and one when the tide was ebbing.

Further analysis into naupliar stages does not reveal any regularity. Fig. 4 shows the occurrence of later-stage nauplii over the same period (naupliar stages III-VI inclusive were counted as 'later-stage' nauplii for *B. balanoides*

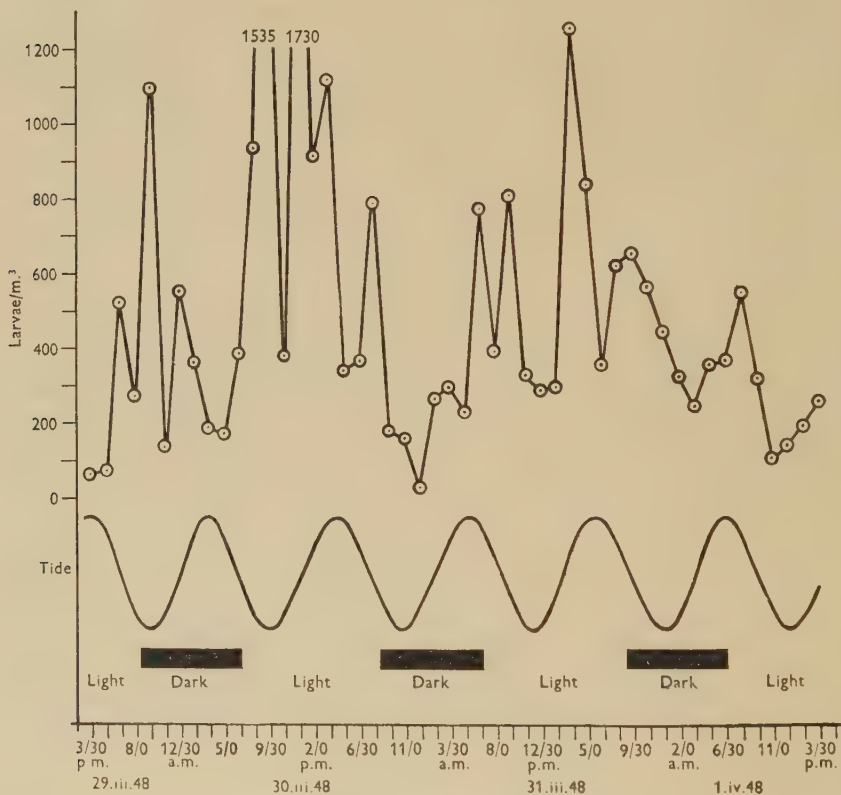


Fig. 3. Total barnacle larvae in the serial hauls of 29 March-1 April.

and *B. crenatus* and naupliar stages IV-VI for *Verruca stroemia*). The only point of interest about this figure is that the numbers of *Balanus balanoides* and *B. crenatus* larvae tend to decrease over the later part of the period, whereas the larvae of *Verruca stroemia* are then definitely more abundant. It is possible that the weather may have been an important factor in producing this result. For the last 24 hr. of this series of hauls, there was a gale from the south and west and it is possible that this churned the water sufficiently to bring numbers of *Verruca* larvae into the surface layers.

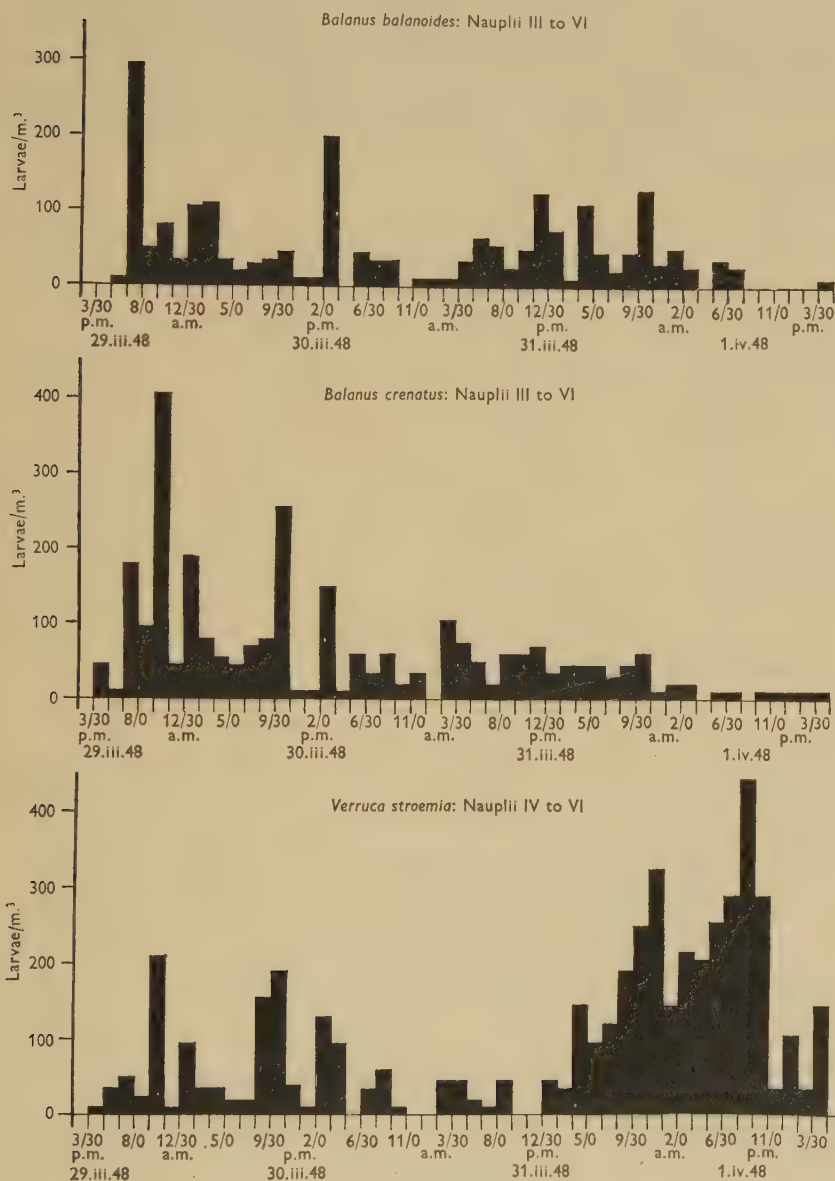


Fig. 4. Numbers of later-stage nauplii, separated into species, for the third set of serial hauls.

Fig. 5 shows the numbers of cyprids obtained in each haul. Here the presence of smaller numbers of larvae near the surface during the night seems to be a genuine result (though a maximum did occur just after dark on 31 March), but the day-time results are most irregular. The cyprid maxima, it will be noted, do not always correspond in time with the naupliar maxima (Fig. 3).

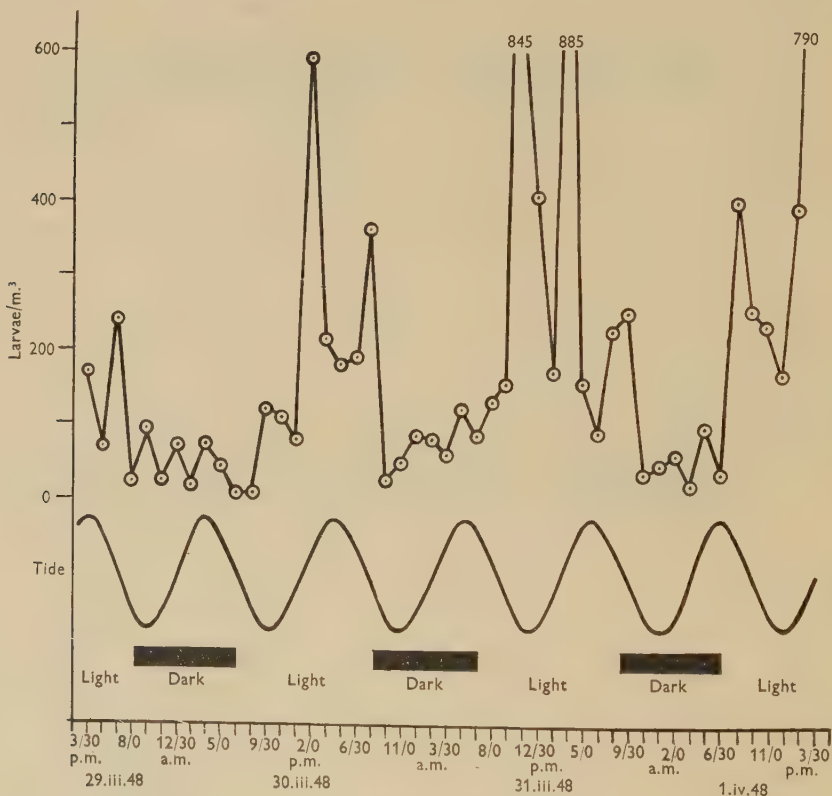


Fig. 5. Numbers of cyprid larvae in the serial hauls of 29 March–1 April.

Other series. Further evidence, of a similar nature to that just described, is provided by two sets of hauls made in 1944. The results are shown in Fig 6. These hauls were made by hauling a plankton net across the bay between Keppel Pier and the north-eastern side of Keppel Point, a distance of roughly 500 ft. The numbers of larvae recorded are not given as numbers/m.³ as these hauls cannot be considered as quantitative. The towing speed used was roughly one knot, but the relative speed of the net varied with the state of the tide. This factor was important because the towing speed was roughly the same as that of the ebb tidal current. An attempt was made to convert the figures

obtained to numbers/m.³, assuming that the fishing efficiency of the net was 100% throughout and that the mouth of the net remained normal to the current throughout the run. The results obtained, however, were so low in comparison with those recorded from the pump hauls just described, as to indicate that these assumptions were not valid.

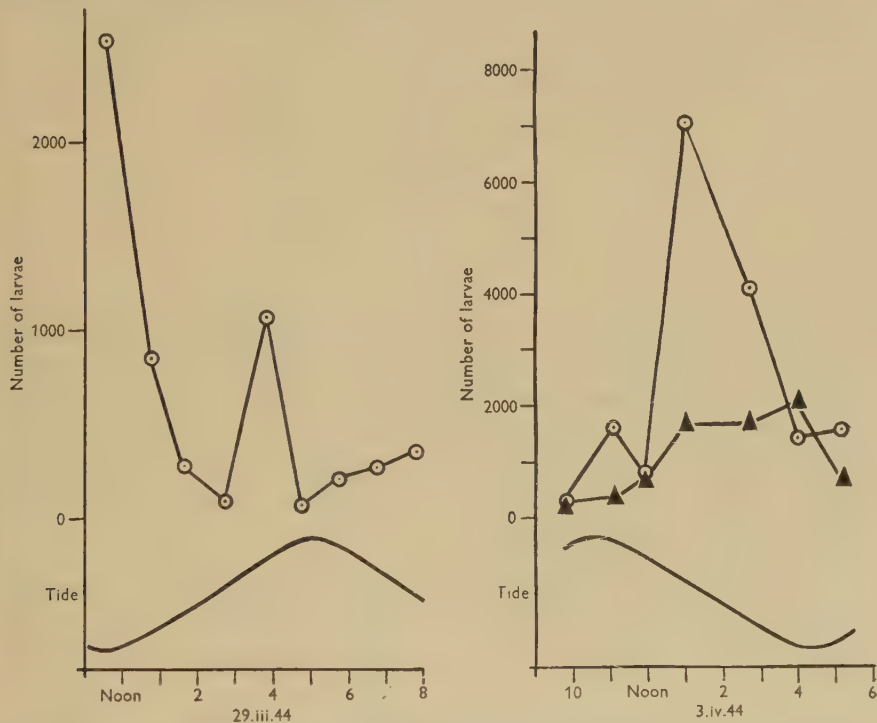


Fig. 6. Total barnacle larvae in the serial hauls of 29 March 1944 and 3 April 1944.
 ○ — ○ Stages I-VI, ▲ — ▲ Cyprid.

The first of this series of hauls was made on 29 March, when many late-stage nauplii and a few cyprids were present; the second was made 5 days later, when cyprids were more abundant. The results obtained on 29 March suggest a maximum number of nauplii at low water and possibly a minimum at high water, but they were contradicted by those obtained on 3 April, when numbers were low both at high and at low water, and a maximum occurred during the ebb. The cyprid maximum, which was ill-defined, occurred at low water.

SUPPLEMENTARY HAULS

In the intervals between the sets of serial hauls described in the last section, a number of other hauls were made, to test the reproducibility of the samples obtained.

One test of this kind was made on 16 March and the results are shown in Table II. It was designed both to investigate how much the larval population varied over very short periods and to compare the results of pump hauls with those of hauls made simultaneously from the pier.

TABLE II. VARIATION IN NAUPLIAR NUMBERS OVER VERY SHORT PERIODS

State of tide	Time (p.m.)	Nauplii/m. ³
Flow	3.00	455
Flow	3.45	715
High water	4.32	905
Ebb	5.03	910
Ebb	5.36	930
Ebb	5.42	610
Ebb	5.57	2060
Ebb	6.08	925
Ebb	6.18	935
Ebb	6.26	910

The numbers of larvae were remarkably uniform after the haul made at 4.32 p.m., with two exceptions, one a particularly striking one. It is interesting to note that, supposing these hauls had been taken at 90 min. intervals (as in the series described in the preceding section), the exceptional haul (5.57 p.m.) would have been the one recorded and the sequence of readings, 3.00 p.m., 4.30 p.m. and 6.00 p.m. would have shown a convincing rise, with the larval numbers roughly doubled at each step.

An even more striking example of a sudden variation was found in the course of hauls made to compare the results obtained by pumping the water through a 'fine' plankton net (150 meshes/in.) and through a 'medium' net (50 meshes/in.). An interval of only 7 min. separated the two hauls; the numbers of larvae which these contained are shown in Table III.

TABLE III. NUMBERS OF NAUPLII FROM WATER PUMPED THROUGH 'FINE' AND 'MEDIUM' NETS (17 MARCH)

Species	Naupliar stages/m. ³											
	I		II		III		IV		V		VI	
	F	M	F	M	F	M	F	M	F	M	F	M
<i>B. balanoides</i>	35	0	120	35	35	235	5	95	0	10	0	0
<i>B. crenatus</i>	1710	25	55	0	0	55	5	100	0	20	0	0
<i>V. stroemia</i>	25	0	85	0	40	0	30	80	20	55	0	0

F indicates 'fine' net (150 meshes/in.). *M* indicates 'medium' net (50 meshes/in.).

It was to be expected that the numbers of the early-stage nauplii would be greater from the 'fine' than from the 'medium' net, but there would seem no reason, except a variation in the larval population, why the numbers of later-stage larvae should vary so markedly, since they should be retained by both nets. It should be added that, as only an aliquot part of each haul was counted,

the smaller variations shown in Table III are probably not significant, but some of the variations (e.g. those of the 4th-stage nauplii) seem great enough to be independent of a sampling error.

Other hauls made in rapid succession indicate that sudden variations can also occur in the numbers of cyprid larvae (Table IV).

TABLE IV. VARIATION IN CYPRID NUMBERS OVER VERY SHORT PERIODS (2 APRIL)

Time of haul (p.m.)	Cyprids/m. ³
3.24	845
3.30	1305
3.35	730
3.39	1350
3.43	1490

As many of the maxima shown in Figs. 1-5 are isolated points, unsupported by a graded series of records on either side, it is evident that the results just quoted suggest that, any maximum should be regarded with considerable suspicion, since its occurrence may merely be a matter of chance rather than an indication of diurnal or tidal variation. Though it would therefore seem reasonable to discount many of the maxima recorded in these figures, the situation is possibly not the same for the evidence of diurnal variation in the numbers of larval stages in the surface water. There is some consistent evidence for the reduction in the numbers of all the larval stages in the surface waters during the hours of darkness and this effect is perhaps most strikingly shown for the cyprids of *Balanus balanoides*.

It is possible that the sudden variations just discussed are due to sampling errors rather than to a true variation in larval numbers. The water was pumped through a net and errors may have arisen because all the catch was not always transferred to the collecting jar. Every effort was made to adopt a similar procedure at each collection, so a significant error would appear to be unlikely. A number of hauls were made in which 1 m.³ was pumped through the net in successive thirds. The variations in the numbers of larvae from these hauls were of a similar order to those from hauls in which only 0.3 m.³ of water was passed through the net. If the cause of the sudden variations had been a sampling error, this grouping of hauls into threes should have accentuated this effect, whereas no indications of accentuation were found.

It must therefore be concluded that sudden variations in the numbers of barnacle larvae do occur and that therefore the results of single hauls may be misleading.

COMPARISONS OF NET AND PUMP HAULS

Plankton nets, both 'fine' and 'medium', were fished from Keppel Pier whenever an opportunity arose during the course of these series of pump hauls. A number of instances are thus available for comparisons between the two methods.

Qualitative comparisons are set out in Table V, in which the percentage composition of the net haul is compared with that of pump hauls made immediately before and immediately after the period for which the nets were fished.

There is evidently a rough qualitative equivalence between the pump and net hauls in spite of the sudden variations which may exist between successive pump hauls. Sometimes considerable differences between the two methods of collection do occur, however (e.g. those on 31 March), and these may be due to the incidence of this factor.

TABLE V. QUALITATIVE COMPARISONS BETWEEN PUMP AND NET HAULS

Date	Percentage composition of haul								
	<i>B. balanoides</i>			<i>B. crenatus</i>			<i>V. stroemia</i>		
	<i>P</i> ₁	<i>N</i>	<i>P</i> ₂	<i>P</i> ₁	<i>N</i>	<i>P</i> ₂	<i>P</i> ₁	<i>N</i>	<i>P</i> ₂
11 March	81.7	73.6	72.7	6.3	8.7	9.2	12.0	17.7	18.1
12 March	55.0	40.9	37.0	23.1	2.4	27.0	21.9	56.7	36.0
24 March	76.8	77.2	72.5	18.5	11.9	17.5	4.6	10.9	10.0
29 March	62.0	63.9	66.6	13.8	19.8	26.9	24.2	16.3	6.5
30 March	59.6	51.1	66.6	36.6	25.9	25.2	3.8	23.0	8.2
31 March	16.4	72.1	41.3	78.3	10.9	50.0	5.3	16.1	8.7
6 April	83.7	86.1	44.6	17.3	13.9	54.7	0	0	0.7
8 April	51.6	51.0	41.6	43.4	47.1	54.0	5.0	1.9	4.4
Average	60.9	64.5	55.4	29.7	17.6	33.1	9.6	17.8	11.6

*P*₁ indicates the pump haul made just before the net haul (*N*), *P*₂ the pump haul made just after the net haul.

These qualitative comparisons are taken a stage further in Fig. 7, which shows the analyses of the net and pump hauls for 11 March and 8 April into the larval stages represented. The set for 11 March is more closely comparable than that for 8 April, but as the numbers of larvae present in the pump hauls for 11 March were considerably greater than those for 8 April, a closer correspondence in the former set was perhaps to be expected.

Quantitative comparisons indicate considerable differences between the numbers of larvae collected by the pump and by nets fished from the pier. It is not possible accurately to estimate the volume of water that passes, or could pass, through a net fished from the pier, but if it is assumed that the current through the pier during the ebb runs at a speed of 1 knot and that all this water passes through the net, then the volume filtered is approximately 365 m.³. It is probable that all the water does not pass through the net, but as

the estimate of current speed is a conservative one (a good ebb will run at a speed of just over 2 knots at Keppel Pier) this allows for some error in the assumption that all the water is filtered through the net.

On these assumptions, comparisons between pump and net hauls have been made and the results are shown in Table VI. The first two estimates in this table were made at a time when *Skeletonema* was very abundant; this was probably an important factor in producing the low fishing efficiencies recorded.

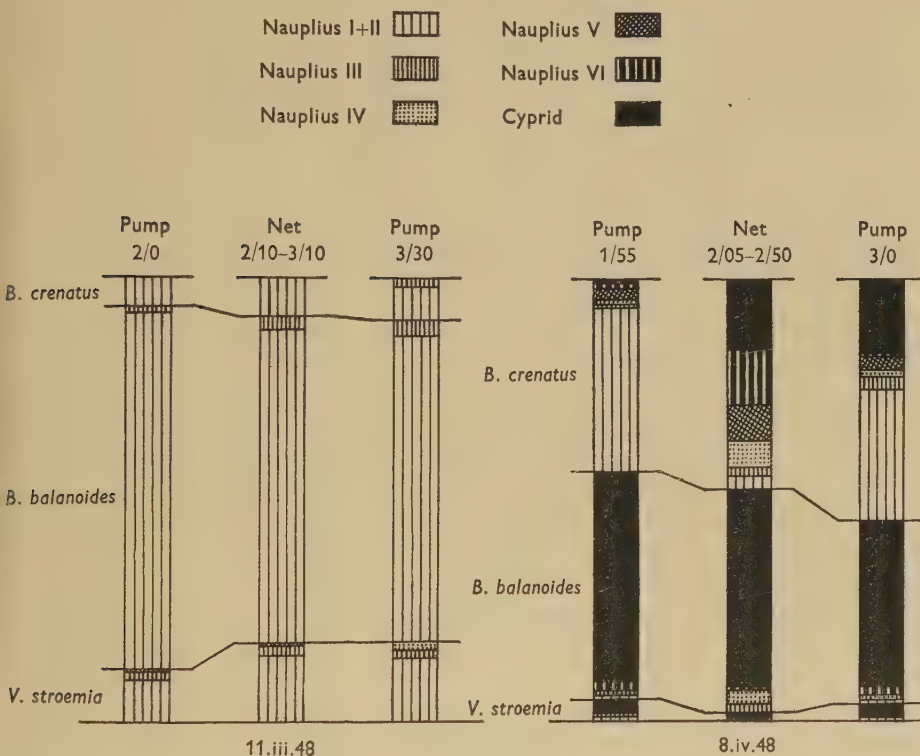


Fig. 7. Analysis of net and pump hauls on 11 March and 8 April.

Though the last three estimates are based on the net hauls from both 'fine' and 'medium' nets, roughly 95% or more of the larvae recorded came from the 'medium' net, so that the fishing efficiencies given may be taken as those of the latter net only.

During a period when diatoms are abundant in the water, clogging of the mesh of the net is doubtless an important factor in reducing fishing efficiency, but at other times clogging of the mesh does not seem to be the most important factor in reducing this efficiency. Nets have usually been fished from the pier for 1 hr. and if clogging were a significant factor the numbers of larvae caught,

for example, during the first 10 min. should be much greater than those caught during the last 10 min. of this immersion period. The experiment was therefore made of subdividing the fishing period into five periods, each of 10 min. duration. At the end of each fishing period, the net was carefully withdrawn and the collecting jar changed with the minimum of disturbance. The results of these hauls are shown in Table VII.

TABLE VI. FISHING EFFICIENCY OF PLANKTON NETS

Date	Range of tide	Total larvae/m. ³ (from pump)	Total larvae (from net)	Theoretical total larvae from net	Fishing efficiency (%)
11 March	Spring	8820	24,200	3,220,000	0.75 (F)
12 March	Spring	5270	5,870	1,923,000	0.30 (F)
24 March	Neap/Spring	315	45,460	229,900	24.9 (F + M)
30 March	Spring/Neap	540	47,400	394,200	12.0 (F + M)
6 April	Neap/Spring	1040	38,980	759,100	5.1 (F + M)

The total larvae/m.³ (from pump hauls) is the average of the haul immediately before and that immediately after the corresponding net haul.

The letters in parentheses after the estimates of fishing efficiency indicate the type of net used; *F* indicates 'fine' (150 meshes/in.) and *M* indicates a 'medium' net (50 meshes/in.).

The numbers of larvae per haul showed a decrease with both nets, the reduction being more marked with the 'fine' net, but there is little in these results to support the suggestion that all the larvae which are recorded at the end of an hour's fishing entered the net in the first few minutes that the net was in the water. A more likely factor in producing low fishing efficiency would therefore appear to be that only a small proportion of the water reaching the mouth of the net is actually filtered through its mesh.

TABLE VII. NUMBERS OF LARVAE IN SUCCESSIVE 10 MIN. NET HAULS

Period	Total larvae	
	'Fine' net	'Medium' net
1	940	3370
2	1700	3160
3	470	3460
4	420	2960
5	360	2220

DISCUSSION

Weiss (1947) has recently investigated the rate of attachment of the cyprids of *Balanus improvisus* and finds that, for this species, there is a definite diurnal variation, attachment taking place more by day than by night. If the number of attachments over a given period is proportional to the number of larvae present in the surface water, then the results of the present study would suggest that the same was true for *B. balanoides*, as the cyprids of this species were more plentiful in the surface waters during the day. It was hoped that it

would be possible to supplement these planktonic investigations by observations on the amount of settlement on collectors exposed on Keppel Pier, but the numbers which attached were too small to allow this direct test to be made.

Diurnal variations in the numbers of cyprids in the surface water is one of the few definite results that have emerged from this investigation as it was originally planned, though it seems likely that all the larval stages, at least of *B. balanoides* and *B. crenatus*, also show some diurnal variation. Weiss (1947) also found that, during the day, the greatest numbers of cyprids attached during the low tide period. No regular variation with tidal state was found for the occurrence of the three species present in the hauls made in the present series, but this difference does not necessarily imply a difference in habit, since Weiss makes it clear that the variation he found seemed to be due to the geographical conditions of his experimental site.

The sudden variations which occur in larval numbers have been clearly shown by these counts of pump hauls; this phenomenon seems to be common to all the stages of the three species of barnacles. Fluctuations between hauls taken in rapid succession have, in the present investigation, probably been emphasized because the volume of water filtered was so small, but their persistence when the volume filtered was trebled and their occurrence in the early stages of the investigation, when the numbers of larvae present were much greater, suggests that the phenomenon cannot wholly be attributed to inadequacy of sampling.

The hauls collected by nets from the pier seem to give a reasonable qualitative impression of the various species and stages of barnacle larvae present in the plankton. As these nets are fished for periods much longer than those required to take a pump haul, the results they give are, in one respect, more reliable than those given by the pump hauls, namely that the longer fishing period will tend to obliterate the sudden fluctuations which characterize the shorter fishing periods. This advantage is certainly outweighed by the low fishing efficiency of the nets themselves.

The low fishing efficiency of the nets seems likely to be produced because only a small proportion of the water which is carried to the mouth actually enters the net. The low fishing efficiencies recorded suggest that the speed of the ebb tidal current may be reduced, near the mouth of the net, to a value which is not far removed from the rate of swimming of the larvae. This may mean that certain stages, or certain species, may be able to avoid capture. In this connexion, it is of interest to note the results presented in Table V (p. 364). The numbers of *B. crenatus* larvae caught in the net are less than those taken by the pump (this difference is mainly due to the increased numbers of 1st- and 2nd-stage nauplii in the latter hauls) and the numbers of *Verruca stroemia* larvae caught by the net are greater than those taken in the pump. No significant differences, however, occur between the pump and net hauls of the larvae of *Balanus balanoides*. These differences may be due to biological factors

such as differences in the rate of swimming or differences in rheotropism; further work on this point may well be interesting.

It should be added that the estimates of fishing efficiency quoted earlier, as they have been expressed numerically, probably give too definite an impression of the results achieved. Considerable variations in fishing efficiency are possible between two successive immersions of the same net, so that an extended series of determinations would have to be made to establish the fishing efficiency of a given net at all firmly.

Biologically, the difference in fishing efficiency between the fine and medium nets is important because it obscures the numerical differences between the various larval stages. The early-stage nauplii chiefly appear in fine net hauls, whereas the later-stage nauplii and cyprids chiefly appear in the hauls made with the medium net. As the fishing efficiency of a medium net appears to be as much as eighty times greater than that of a fine net, an incorrect impression of larval mortality and dispersal during the sequence from hatching to settlement is obtained. Table VIII, below, gives the highest numbers of each larval stage of each species recorded during the present series of pump hauls.

TABLE VIII. HIGHEST NUMBERS OF LARVAL STAGES
(NUMBER/M.³) FROM PUMP HAULS

Species	Larval stage						Cyprid
	Nauplius						
	I	II	III	IV	V	VI	
<i>B. balanoides</i>	112,570	10,285	235	230	350	230	1085
<i>B. crenatus</i>	3,430	2,000	70	190	70	70	145
<i>V. stroemia</i>	2,285	915	995	285	430	60	65

These results suggest that roughly 1% of the larvae of *B. balanoides* which are hatched survive to become cyprids, roughly 9% of the larvae of *B. crenatus* and roughly 3% of the larvae of *Verruca stroemia* complete the larval sequence. This is, however, only the crudest approximation, since it leaves out of account the life period of each larval stage (this is possibly the reason why the cyprid numbers are higher than those of the 6th-stage nauplii), and it also assumes that the three species can be fairly compared. This is probably not true, as these pump hauls were started at a time when the larvae of *Balanus balanoides* were hatching, and thus very large numbers of the early-stage larvae of this species were recorded, but the pump hauls were started too late to record the corresponding hauls of the early-stage larvae of *B. crenatus* and *Verruca stroemia*.

SUMMARY

Records are given of the numbers of barnacle larvae obtained from samples of water pumped through a plankton net. Several series of hauls were made at intervals over the time of year when barnacle larvae are abundant.

The numbers of the cyprid larvae of *Balanus balanoides* in the surface waters show a diurnal variation, being markedly less during the hours of darkness. This conclusion may also apply to the cyprids of *B. crenatus* and *Verruca stroemia*, but the numbers of these larvae were too small to permit reliable conclusions to be drawn. There is some evidence that similar diurnal variations occur in larval stages other than the cyprid.

The numbers of larvae present in the surface waters during the day showed marked variations which were not correlated with tidal state. Pump hauls made within a few minutes of each other showed comparable variations.

Comparison of the hauls made using the pump and those from nets fished in the ebb tide suggest that the latter give an adequate qualitative record of the barnacle larval stages present, but are inadequate quantitatively. The fishing efficiency of a 'fine' net (150 meshes/in.) is very low, values of less than 1% being recorded, and that of a 'medium' net (50 meshes/in.) is not high, the maximum value recorded for this type of net being roughly 25%. There are indications that loss of fishing efficiency is produced by water not entering the net rather than by clogging of the mesh. The latter factor is undoubtedly important, however, in producing the very low fishing efficiency of a 'fine' net during a period of diatom abundance.

The difference in fishing efficiency between 'fine' and 'medium' nets affects estimates of the numbers of each of the larval stages present, since most of the early-stage nauplii appear in 'fine' net hauls, whereas most of the later-stage nauplii appear in 'medium' net hauls. Pump hauls seem likely to present a more accurate record and estimates of the success of the larval sequence based on these hauls suggests that only 1% of the first-stage nauplii may complete the full sequence of development to the cyprid stage.

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CERTAIN EFFECTS OF AGITATION UPON THE RELEASE OF PHOSPHATE FROM MUD

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INTRODUCTION

Studies of the phosphate concentration of sea water are of primary importance in assessing the potential productivity of the sea (Sverdrup, Johnson & Fleming, 1942; Harvey, 1945). Amongst the factors governing these concentrations, the role of the bottom deposits has been largely neglected. There is an impression (Marshall, 1947) based upon analyses of marine muds by Moore (1930) and estuarine deposits by Stockfisch & Benade (1930), that the surface layers of bottom deposits contain large amounts of phosphate. If so, the factors controlling the exchange of phosphate between mud and sea water are of interest. This investigation concerns one of these factors, and later papers will deal with others.

The work has been carried out in the laboratory because, although conditions are artificial, they are relatively controllable, and it is easier to distinguish the significant factors. Estuarine muds have been used in preference to offshore deposits because of their accessibility and because they are more likely to withstand laboratory conditions without catastrophic biological change. Analyses were made throughout upon sea water in contact with mud, thereby avoiding the difficulties of determinations upon mud itself.

METHODS

Phosphate determinations. Atkins's (1923) modification of Denigès method was used, employing Atkins's original reagents. Molybdate solution (1 ml.) and two drops of stannous chloride solution were used per 100 ml. sample, and colours compared visually using Hehner or Nessler tubes. Comparisons were initially made in daylight, but it was suspected that variations in spectral composition were altering the salt errors (Cooper, 1938) and so all results below were determined in artificial light in a dark room. Tubes were viewed with standards alternatively right and left of the unknown (Matthews, 1916) and each time a value just above and just below the 'true' value was recorded. Finally the mean of the four values was noted. Salt errors were determined as described by Ibañez (1933), and the factor varied between 1.33 and 1.37 for

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sea water, and between 1.15 and 1.18 for samples diluted with an equal volume of distilled water. Reagent blanks were determined as described by Cooper (1933) and allowances were made for salt errors in these blanks. Harvey (1948) has shown, in a paper published since this work was completed, that with stored reagents, blanks are largely due to silicomolybdate formation, and are not subject to salt errors. The results are thus too low by amounts up to about 2 mg. $P_2O_5/m.^3$. The experimental error is estimated at about ± 2 mg./m.³, and any arsenate present is included as phosphate (Atkins & Wilson, 1927).

Mud. A scraping of the top centimetre of mud, containing *Corophium*, was collected on 11 December 1946 from mid-tide level on the south bank of the River Blyth, close to the Fever Hospital. Sand and grit were removed by washing, and sea water, mud, silt, and *Corophium* were added to a greenish glass tank (35 × 27 × 35 cm.) in a shaded corner of the laboratory. The solids settled as a loose brown layer about 7 mm. thick, and were kept for about a month before the experiments started.

Filtration. With turbid liquids, filtration was essential. Whatman No. 542 papers were used and the first 20 ml. of filtrate discarded. Distilled water, sodium chloride solution, and dilute sodium bicarbonate solution extracted no phosphate from these papers or from the glassware.

pH *determinations* were performed colorimetrically, and the results, after correction for salt errors, are accurate to about the nearest 0.05.

RESULTS

Preliminary experiments

Sea water in contact with settled mud was analysed. After stirring for 5 min., samples were pipetted at intervals from the middle of the water column, filtered, and analysed. Typical results are given in Table I, and these show, first,

TABLE I

8/9 January 1947; P_2O_5 at 23.00 hr. G.M.T., 125 mg./m.³; stirred 23.15–23.20 hr.

Interval between stirring and collection of sample (min.)	Duration of filtration (min.)	P_2O_5 (mg./m. ³)
0	15	111
75	15	110
120	10	120
195	15	122
240	15	109
265	15	123
460	15	112

considerable variation in phosphate concentration, and secondly that this concentration has decreased. Later experiments gave both increases (Table III) and decreases (Table II) in concentration.

Ultrafiltration

In the above experiment only the original sample was unfiltered, and particulate or colloidal material may have increased its phosphate concentration. To evaluate the significance of a colloidal fraction, sea water and mud were stirred, then filtered, and then ultrafiltered through a collodion membrane. After ultrafiltration the phosphate should be reduced by an amount equivalent to that released from the colloids.

Collodion ultrafilters were prepared round a 2.5 cm. boiling tube from the following mixture: 7.0 g. dry pyroxylin, 100 ml. absolute alcohol, 100 ml. ether, 4.8 g. ethylene glycol. A first coat was applied at 20° C. and dried for approximately 3 min., and a second similar coat added. A third coat was allowed to dry at 20° C. for about 10 min., and then at 15° C. for about 2½ hr. The membrane was removed from the tube after standing in water for 1 hr. Many membranes were made similarly, but mostly burst under high pressures. Those finally selected withstood a pressure of 600 mm. Hg and filtered Congo Red from aqueous solution. During ultrafiltration, a pressure of 500–550 mm. Hg was used.

Sea water and mud were stirred, and two samples collected, one for normal filtration, and the second for normal filtration followed by ultrafiltration. Analyses showed (see Table II) that the ultrafiltered samples gave the *greater* phosphate concentrations. These increases were not due to evaporation of water, as chlorinities increased only by 0.5% during ultrafiltration.

TABLE II

9/10 January 1947; P₂O₅ at 23.00 hr. G.M.T., on unfiltered unstirred sea water, 123 mg./m.³; stirred 23.15–23.20 hr.

Interval between stirring and collection of sample (min.)	Duration filtration (min.)	P ₂ O ₅ (mg./m. ³)	Duration ultrafiltration (min.)	P ₂ O ₅ (mg./m. ³)
0	15	115	—	—
0	40	—	125	149
2	10	120	—	—
2	35	—	139	145

In the next experiment, sea water was stirred with mud, filtered, and analysed. Half the filtrate was ultrafiltered, and the remainder left standing in a covered beaker for the duration of ultrafiltration. The results (Table III) confirm the increase in phosphate on ultrafiltration, and show that when filtered samples stand in glassware, a marked reduction in phosphate concentration may occur. The anomalous effects of ultrafiltration might be complicated by changes on storage, and these were therefore investigated.

TABLE III

10/11 January 1947; P_2O_5 at 23.00 hr. G.M.T., 118 mg./m.³; stirred 23.15–23.20 hr.

Interval between stirring and collection of sample (min.)	Duration filtration etc. (min.)	P_2O_5 (mg./m. ³)	Duration ultrafiltration (min.)	P_2O_5 (mg./m. ³)
0	45	150	420	155
	as last, stood for 420 min.	138	—	—
465	105	145	180	175
	as last, stood for 180 min.	126	—	—

Phosphate Changes in Stored Filtrates of Muddy Sea Water

General Nature of Changes and Effects of Bactericidal Agents

A litre of filtrate was analysed, and three samples of 250 ml. set aside in 350 ml. conical flasks. One was kept as control, while to the others were added 1 ml. of 40% formaldehyde and 1 ml. of chloroform respectively. Analyses were performed at intervals, and the results (Table IV) show that storage in glassware produces an increase in phosphate concentration, followed by a decrease to the original value or even lower. These changes are prevented by formalin or chloroform.

TABLE IV

15/16 January 1947; stirred 21.30 hr. G.M.T.; filtered 21.35–02.15 hr.; P_2O_5 of filtrate then 111 mg./m.³; bottles below filled 02.20 hr.

Time from filling bottle (min.)	P_2O_5 (mg./m. ³)		
	Control	1/250 formalin	1/250 chloroform
40	117	109	111
100	127	111	109
160	122	108	109
220	115	108	109
280	108	109	110

Similar results were obtained in an experiment of longer duration using 500 ml. samples in 1 l. bottles (Table V). These results confirm the increase in phosphate concentration, and also show that on prolonged standing the phosphate concentration decreases to below the original value. It should be noted that while the results given in Tables IV and V are similar, the changes are less marked in the latter. Further experiments confirmed both the initial increase and subsequent decrease, for example in one experiment phosphates increased from 111 to 144 mg./m.³ on standing for an hour, and in another they decreased from 100 to 2 mg./m.³ on standing for 18 hr. The results in Table V also confirm that both formalin and chloroform prevent both the increase and decrease in values, and further work showed that a 1/250 concentration of toluene had a similar effect.

TABLE V

17 January 1947; stirred 09.30 hr. G.M.T.; filtered 09.30-10.10 hr.; P_2O_5 of filtrate then 97 mg./m.³; bottles filled 10.30 hr.

Time from filling bottles (hr.)	P_2O_5 (mg./m. ³)		
	Control	1/250 formalin	1/250 chloroform
1	104	98	97
2	101	98	99
3	101	99	98
4 $\frac{1}{2}$	98	97	98
5 $\frac{1}{2}$	98	96	95
6 $\frac{1}{2}$	90	96	96
7 $\frac{1}{2}$	86	95	95
8 $\frac{1}{2}$	84	95	96
9 $\frac{1}{2}$	84	94	95

The increase in concentration probably explains the high values after ultrafiltration because this process takes about the same time as the attainment of maximum values on standing. Rise and fall are prevented by bactericidal agents, and this suggests that living organisms in the filtered samples are responsible.

Changes in the Physico-Chemical Environment

Both rise and fall in phosphate concentration can occur during night or day, and when temperatures are either rising or falling (within the range 11.0-17.5° C.). The phenomena are not independent of temperature, since the fall at least is greatly retarded by low temperatures. For example, an original phosphate concentration of 105 mg./m.³ immediately after filtration was reduced after 19 hr. at 13-14° C. to 2 mg./m.³, but a parallel sample at 0° C. was only reduced to 87 mg./m.³.

The phosphate increase on storage is accompanied by a small increase in pH, but the subsequent decrease occurs without further pH change (Table VI).

TABLE VI

17 January 1947; stirred 09.30 hr. G.M.T.; filtration 09.30-11.10 hr.; solution stored in Winchester.

Time elapsed after filtration (min.)	P_2O_5 (mg./m. ³)	pH
10	91	7.4
70	118	7.5
130	109	7.55
190	109	7.6
250	108	7.6
310	108	7.6
370	107	7.6

A filtrate of muddy sea water was poured into bottles, hydrochloric acid or sodium bicarbonate solution added, and the whole thoroughly shaken. (The

acid and bicarbonate contained negligible quantities of phosphate.) The results of a short experiment (Table VII) show that increasing the pH augments the rise in phosphate, while decreasing it has virtually no effect.

TABLE VII

20 January 1947; stirred 10.50–10.55 hr. G.M.T.; filtration 10.55–12.10 hr.

Interval between filtration and collection of sample (min.)	Alkaline		Control		Acid (1)		Acid (2)	
	P ₂ O ₅ (mg./m. ³)	pH	P ₂ O ₅ (mg./m. ³)	pH	P ₂ O ₅ (mg./m. ³)	pH	P ₂ O ₅ (mg./m. ³)	pH
5	—	8.8	121	7.4	—	6.6	—	6.4
10	—	—	—	7.45	—	—	—	—
110	141	8.8	126	7.8	128	6.7	129	6.5

For longer experiments, considerable volumes of filtrates are needed, and filtration takes so long that most of the rise in phosphate concentration has passed. When filtered samples are stored overnight, however, and the phosphate accordingly reduced, this can be regenerated by shaking. Vessels half full of liquid were shaken by hand for 5 min., and the subsequent changes in phosphate concentration were exactly similar to those observed after filtration (see control sample, Table VIII). This is of great interest, and suggests that the normal initial rise in phosphate may be due to mechanical agitation of the mud and sea water.

Further work upon the effect of pH was performed upon the changes occurring when filtered stored sea water is reshaken by hand for 5 min. Results are given in Table VIII, and these, in addition to demonstrating the effects of agitation, show that: (a) increases in pH augment the initial phosphate rise, but decreases have only a very slight effect; (b) pH changes have little effect on the subsequent fall in phosphate concentration.

TABLE VIII

20 January 1947; stirred 10.50–10.55 hr. G.M.T.; filtered 14.30–18.00 hr.; stored overnight at 8° C. At 09.35 hr. 21 January, P₂O₅, 98 mg./m.³. At 09.40 hr. poured into flasks, acid and alkali added except to control; all shaken till 09.45 hr.

Interval between shaking and collection of sample (min.)	Alkaline		Control		Acid (1)		Acid (2)	
	P ₂ O ₅ (mg./m. ³)	pH	P ₂ O ₅ (mg./m. ³)	pH	P ₂ O ₅ (mg./m. ³)	pH	P ₂ O ₅ (mg./m. ³)	pH
5	—	9.1	—	7.9	—	6.8	—	6.2
65	125	9.01	102	7.9	103	6.8	103	6.2
125	148	9.1	115	7.9	120	6.8	125	6.2
185	119	9.05	104	7.9	116	6.9	125	6.3
305	103	9.05	78	7.8	100	6.9	102	6.3
365	94	9.05	70	7.8	85	6.9	88	6.25
After 385 min. (at 16.10 hr. G.M.T.) all shaken for 15 min.								
25	119	9.05	89	7.85	95	6.9	87	6.3
85	105	9.05	74	7.8	89	6.9	104	6.2

Size of the Containing Vessel

At various times, different-sized bottles of different types of glass were used for storage. The changes were similar for all types, but seemed greater with small vessels. (Compare, for example, the results in Tables IV and VI.) The effect of the size of the bottle was therefore investigated, using bottles of similar shape, and made of similar (white) glass. The results (Table IX) show that both rise and fall in phosphate values are greater in smaller vessels.

Recovery of Phosphate after Disappearance on Long Standing

After standing overnight at 14° C. the phosphate concentration of a filtered sample of muddy sea water was reduced from 105 to 2 mg./m.³. About one-third of the phosphate which had disappeared was recovered from the containing vessel after treatment with distilled water on a water-bath for 1½ hr. None was obtained from the liquid after boiling for 1½ hr.

TABLE IX

4 January 1947; stirred 09.20–09.25 hr. G.M.T.; filtered 09.25–11.10 hr. At 11.40 hr. P₂O₅, 97 mg./m.³. At 11.45 hr. all bottles filled to depth of 7 cm. and shaken vigorously till 11.50 hr.

P₂O₅ in mg./m.³ in bottles of different sizes (diameter, cm.)

Interval between filling bottle and collection of sample (hr.)	5.6	7.1	8.0	9.7
	Area in contact with liquid (cm. ²)			
	c. 148	c. 196	c. 226	c. 291
1	107	101	99	97
3	105	102	98	98
5	100	100	96	94
.23	75	81	92	92

DISCUSSION

Preliminary experiments on the effect of agitation upon the exchange of phosphate between estuarine mud and sea water gave variable results. Sometimes phosphate was evolved, and sometimes absorbed by the mud. It was suspected that colloidal material in the samples was introducing complications, and that removal of colloids would reduce the apparent amounts of inorganic phosphate present. On the contrary, removing the colloids was accompanied by an *increase* in phosphate concentration.

A similar increase occurs, however, when filtered sea water stands in glassware for the duration of ultrafiltration, and this obscures any possible effects of colloids. The increase is not due to phosphate leaching from the glassware, and implies the conversion of a precursor into 'Denigès active phosphate'. This process is more obvious in small containing vessels, which is reminiscent of the effects of size of the containing vessel upon the growth of bacterial populations in stored sea water (ZoBell & Anderson, 1936; Lloyd, 1937; ZoBell, 1946, p. 83). It is also prevented by bactericides. Redfield, Smith & Ketchum (1937) have shown that bacteria will pass extremely fine filters, and

Dr H. W. Harvey also informs me (personal communication) that cells up to 3μ in diameter can pass the filters here employed. It appears, therefore, that the above liberation of phosphate is due to the activity of living organisms, but work at present in progress shows that large quantities of phosphate can be freed from animal tissues solely as a result of enzymes in the tissues themselves.

On more prolonged storage, phosphate disappears from solution, and is probably mainly immobilized on the walls of the containing vessel. This removal is slowed by cold and bactericides, and depends on the size of the vessel. This suggests that living organisms are also responsible for the removal of phosphate. After this removal, phosphate can be regenerated by shaking the vessel, and if the previous reduction in concentration is due to removal by bacteria, regeneration is likely to be due to destruction of bacteria, and release of phosphorus-containing compounds.

The similarity between the phosphate release on shaking a filtrate and the initial release when muddy water is filtered suggests that, in the latter process, phosphate is also derived from the protoplasm of destroyed organisms. It is impossible to say whether these are destroyed by the stirring of the mud and water or by the filtration which follows. Probably both processes assist in phosphate release.

Waksman, Stokes & Butler (1937) and Renn (1937) have shown that phosphate is rapidly regenerated from autolysing bacteria, but as they dealt with large bacterial populations, with different proportions cytolysing at any given time, there is no indication of how long it takes for an individual cell to free its phosphate. Under present conditions this process seems to take about 2 hr. to be completed.

The following hypothesis explains the observed facts:

(i) When mud and sea water are mixed by stirring, or when muddy sea water is filtered, or when the filtrates are agitated, bacteria are destroyed.

(ii) Their protoplasm, rich in phosphorus, is broken down by living bacteria, with release of phosphate.

(iii) The bacteria grow, using the remaining organic matter, now poor in phosphorus.

(iv) During growth, they reabsorb the phosphate previously released.

The overall effect is therefore of phosphate absorption by the bacteria. Renn (1937) and Waksman *et al.* (1937) have already shown that when sea water is incubated in the dark, for the first day or two phosphate is absorbed. Work at present in progress has often given similar results.

This work has been solely concerned with exchange of phosphate between a surface scraping of aerated mud and sea water. Similar results have been obtained with several samples of aerated muds and silts, but there are preliminary indications that oxygen-free muds give different results.

SUMMARY

When sea water is stirred with mud and then filtered, its phosphate concentration may either increase or decrease. When the filtrate is ultrafiltered, the concentration increases.

Similar increases occur when the filtrate is stored in glassware, and these obscure any effects of the presence of colloidal material. On storage concentrations rise for about 2 hr., and then fall to as low as 2 mg./m.³ P₂O₅ in 18 hr.

Rise and fall are both prevented by the addition of formalin, chloroform or toluene, and are more noticeable in small containing vessels. Both occur during either day or night, and when temperatures are either rising or falling.

The increase in phosphate is accompanied by a small increase in pH and is augmented by an increase in pH value.

When a filtrate of muddy sea water is kept overnight, and the phosphate concentration reduced, phosphate can be regenerated by shaking.

The phosphate which disappears on long-standing is largely immobilized on the walls of the vessel.

It is suggested that these changes are due to: (i) destruction of organisms by agitation with release of protoplasm; (ii) breakdown of this protoplasm by bacteria with release of phosphate; (iii) absorption of phosphate by bacteria growing on the walls of the vessel.

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BRITISH FOLLICULINIDAE (CILIATA, HETEROTRICHIA)

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(Text-figures 1-3)

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INTRODUCTION

The Folliculinidae are a well-marked family of heterotrichan ciliates, most of which are marine and have a world-wide distribution. They are abundant in most marine aquaria, while in the sea they are usually found attached to Algae, Polyzoa, Crustacea, Mollusca, tube-building Annelida or tests of Tunicata, down to a depth of about 5 fathoms. The family is characterized by: (a) the blue or bottle-green colour of the body; (b) the large bilobed peristomial field; (c) secretion of a case in the form of a bottle or flask; (d) the two phases in its life, one sedentary and the other migratory; and (e) dedifferentiation of the adult to form the migratory phase and its reorganization into the sedentary phase.

Since the latest publication on British Folliculinidae (Das, 1947*b*), the present author had the opportunity of examining six species of Folliculinidae during his stay in Great Britain. If the records by other workers of *Folliculinopsis ampulla* (Müller) be correct, and if *Parafolliculina hirundo* (Kent) be included, we now have eight definite species of British folliculinids; whereas until 1946 only three species were known. An attempt has been made in this paper to give complete, and for most revised, descriptions of these eight species. The classification followed here is after Fauré-Fremiet (1936*b*), who has shown that many of the genera listed by Kahl (1932, 1933) are not based on well-marked anatomical characters but on the case or lorica alone. Besides, many of the original descriptions by Kent (1881-82) require revision on the basis of work done since then. The characters used for differentiation of species

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are: (i) the size and shape of the case and the body; (ii) the nature of the macronucleus; (iii) the structure of the cell-body; (iv) the colour and nature of pigment; (v) the ciliary bands; (vi) the peristomial lobes; and (vii) the shape and structure of the larva along with the nature of metamorphosis.

HISTORY OF OUR KNOWLEDGE OF BRITISH SPECIES

Our knowledge of British Folliculinidae dates back to 1880, when Wright (1858-9, 1862) described a species as *Lagotia viridis*. Stein (1867) showed that the *Folliculina* of Lamarck (1816), *Lagotia* of Wright (1858), and *Freia* of Claparède & Lachmann (1858), were identical; and thus the prior name *Folliculina* was finally adopted. Wright's species were mostly from Ireland, and it is doubtful if any definite species from England, Scotland or Wales was described by him. Saville Kent (1881-82, pp. 596-601) listed six species, of which only one is definitely British, viz. *F. ampulla* Müller from Falmouth. If, however, we include the Channel Islands then another species, *Parafolliculina hirundo* (Kent, 1882), may be added. Little work was done on the family in Great Britain for the next 50 years. Orton (1930) recorded *Folliculina ampulla* from Plymouth, Fowell (1944) *F. viridis* from Swansea, and Bruce (1935) *F. ampulla* and *F. elegans* from the Isle of Man. The only recent additions to our knowledge of British Folliculinidae are two notes in *Nature* by Das (1947*a*) and by Fowell (1947), and a paper on the biology of some folliculinids by Das (1947*b*) in which a tentative key of the British species is added at the end. Only six British species are listed in the last-mentioned paper, whereas sixteen species are known from the continent (Fauré-Fremiet, 1936*b*) and ten from U.S.A. (Andrews, 1944). Besides the six species already recorded (*Folliculinopsis producta*, *F. ampulla*, *Folliculina simplex*, *F. elegans*, *F. viridis*, and *Parafolliculina hirundo*), two further species, *Folliculinopsis elongata* n.sp. and *F. andrewsi*, can now be added to the list of British species.

DESCRIPTIONS OF SPECIES

Genus *FOLLICULINOPSIS* Fauré-Fremiet, 1936

The genus *Folliculinopsis* was erected by Fauré-Fremiet (1936*b*) to include those folliculinids which have a multiple macronucleus (i.e. like a string of beads). Before this genus was constituted the different species of *Folliculina* were distinguished with difficulty, as forms with simple and with multiple macronucleus were both included in the same species. Then, again, the delineation of species according to shape, size and colour of the case and of the body led to confusion amongst different workers. Individuals of the same protozoan species do not vary with regard to the simple or multiple character of the nucleus, but Kahl (1932) lists multinucleate forms under three separate genera—*Folliculina*, *Pebrilla* and *Mirofolliculina*—while, on the other hand,

both uni- and multinucleate forms are lumped together in *Folliculina ampulla*. I consider the erection of the genus *Folliculinopsis* as an important step forward in the classification of Folliculinidae.

***Folliculinopsis producta* (Wright) (Fig. 1A)**

Folliculina producta Wright, 1858

Folliculinopsis producta Fauré-Fremiet, 1936*b*

DIAGNOSIS

Size and case: large size, total length of extended animal 1000–1500 μ ; tube of case 500–600 μ long, not more than three times the length of the ampulla and having about eight to fourteen spiral thickenings on its wall. *Nucleus* multiple; consisting of a string of about fourteen beads, extending from near the cytopharynx to the junction of the body with the peduncle in the retracted condition of animal. *Cell-body* with peduncle long and narrow, tapering gradually up to its attachment on the ampulla; cell-body broadening in the proximal half and remaining of the same width up to base of peristomial lobes. *Pigment*: colour of animal deep greenish blue (inky, blue predominating); pigment as granules arranged in definite rows throughout body, alternating with the ciliary bands. *Ciliary bands*: about fifty on body, eight on peduncle, and six on each peristomial lobe. *Peristomial lobes* are slender attenuated ribbons, tapering at the free end but without a sharp point; V-shaped process at junction of lobes; each lobe is about half as long as the tube. *Larva* elongated and vermiform; posterior extremity rounded; size $200 \times 75 \mu$; dark blue colour concentrated at oral extremity.

LOCALITY

Plymouth (first record); Cullercoats (Das, 1947*b*); attached to Algae and dead *Pecten* shells from sublittoral region.

REMARKS

See remarks on the next species.

***Folliculinopsis elongata* n.sp. (Fig. 1B)**

Folliculina producta Wright, 1858, *in part*

Folliculinopsis producta Wright var. *elongata* Das, 1947*b*

DIAGNOSIS

Size and case: gigantic size, length 2000–3000 μ when fully extended; shape of case resembles a hockey-stick; tube 1000–15000 μ long and not less than four times the length of the ampulla; eighteen to thirty spiral thickenings on wall of tube. *Nucleus* multiple; consisting of a string of about sixteen to twenty beads. *Cell-body* attached to ampulla by a distinct narrow peduncle which extends beyond the ampulla in the relaxed condition; body fairly broad at free end. *Pigment*: colour of animal deep bluish green (green predomi-

nating); pigment granules arranged uniformly in rows alternating with ciliary bands throughout body. *Ciliary bands*: about fifty on body, eight on peduncle and six or less on peristomial lobes. *Peristomial lobes* are slender attenuated

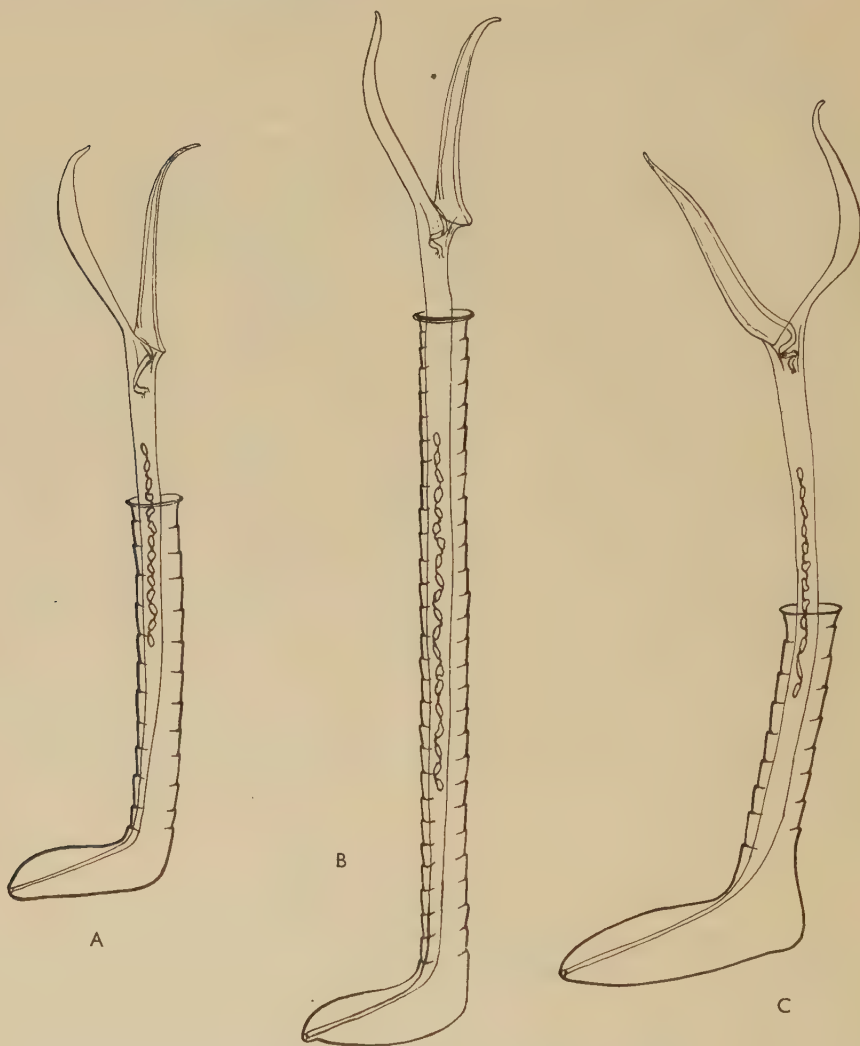


Fig. 1. A, *Folliculinopsis producta* (Wright), $\times 100$. B, *F. elongata* n.sp., $\times 70$. C, *F. andrewsi* (Hadži), $\times 150$.

ribbons, tapering but without a sharp point at tip; V-shaped process at junction of the two lobes much exaggerated; each lobe is less than one-third the length of the tube. *Larva* pear-shaped with posterior end bluntly pointed; size $300 \times 150 \mu$; dark opaque green colour at oral extremity; secretion of case

by attached, elongated larva with three regions—a head, a neck, and an elongated body; the spiral thickenings of the tube are formed by a special spiral band of cilia on the neck of the larva.

LOCALITY

Cullercoats (Das, 1947*b*); attached to tests of *Ciona intestinalis* and to various algae.

REMARKS

The present species was described by me (1947*b*) as *Folliculinopsis producta* Wright var. *elongata*. Since then I have had the opportunity of examining large numbers of specimens resembling *F. producta*, both at Cullercoats and at Plymouth. I can now definitely state that the differences tabulated by me (1947*b*, p. 443) are of a constant character. For example, I examined over a hundred specimens of *F. producta* at Plymouth, and not one of them showed more than fourteen or less than eight spiral thickenings of the case, while almost all the Cullercoats specimens had eighteen to thirty spiral thickenings, the average number being twenty-four. The *F. elongata* forms have been found only at Cullercoats, and I believe this to be a definitely northern species. The differences between *F. producta* and the new species *F. elongata* are even more marked than those between *F. producta* and *F. andrewsi*, the species described next, which has only five to eight turns of the spiral. It may be pointed out here that the gigantic *F. elongata* has not been reported by Andrews (1942, 1944) from U.S.A., and that some of the sketches of Kent (1882) which resemble this species, are superimposed tubes of two successive larvae and not one individual lorica. Both *producta* and *elongata* are multinucleate and thus they must be placed in the genus *Folliculinopsis*.

***Folliculinopsis andrewsi* (Hadži) (Fig. 1C)**

Folliculina producta Wright, 1858, *in part*

F. producta Andrews, 1923

Metafolliculina andrewsi Hadži, 1938

Folliculinopsis producta Andrews, 1942

DIAGNOSIS

Size and case: fully extended animal 600–1000 μ long; case shaped like a sock; tube a little longer than ampulla and having five to eight spiral thickenings on its walls. *Nucleus* multiple; string of about twelve beads. *Cell-body* with peduncle long, narrow and tapering proximally, body ribbon-shaped when extended and about double the length of the tube. *Pigment*: greenish blue colour (much lighter than in *F. producta*): pigment granules uniformly distributed in rows. *Ciliary bands*: peduncle with nine to ten, body with 100, and peristomial lobes with seven to eight bands. *Peristomial lobes* are elongated, ribbon-shaped, tapering distally into a pointed but not sharp tip;

each lobe is only a little shorter than the tube. *Larva* elongated, vermiform, size $200 \times 50 \mu$; posterior end rounded; bluish pigment concentrated at anterior end.

LOCALITY

Plymouth and Cullercoats (first record for Great Britain); attached to dead *Pecten* shells from 3 fathoms, and on test of *Ascidiella aspersa*.

REMARKS

The *Folliculina* described by Andrews (1923, 1942) was referred to Hadži (1938), who described it as a species distinct from *Folliculinopsis producta* Wright, and named it *Metafolliculina andrewsi*. As this species is multinucleate the name *Metafolliculina* should give place to *Folliculinopsis*. I have compared the specimens from Plymouth and Cullercoats, with those described by Andrews and Hadži and have no hesitation in placing them in this species.

If we take the test or case alone into consideration, the present three species of *Folliculinopsis* appear to form a progressive evolutionary series. *F. andrewsi* is the simplest with only five to eight spiral turns on the tube; *F. producta* comes next with its eight to fourteen spirals; and finally the *F. elongata* tube is not only enormous in length, but has eighteen to thirty spiral turns on its walls. Similarly, the number of beads in the nucleus also shows progressive increase.

***Folliculinopsis ampulla* (Müller) (Fig. 2)**

Folliculina ampulla Müller, 1854, *in part*

Folliculinopsis ampulla Fauré-Fremiet, 1936b

DIAGNOSIS

Size and case: length of extended animal about 600μ ; case $300\text{--}500 \mu$ long and usually ridged at its mouth; ampulla flask-shaped, swollen, and large; tube plain and much shorter than ampulla. *Nucleus* multiple; string of twelve to fourteen beads. *Cell-body* with peduncle short and thin, body proper stout in middle and narrowed proximally as well as distally. *Pigment*: blue-green in colour. *Ciliary bands* not known. *Peristomial lobes* of two equal lobes, each leaf-like with short pointed tips. *Larva*: characters unverified.

LOCALITY

Plymouth (Orton, 1930); Port Erin (Bruce, 1935); Cullercoats (Bull, unpublished record, Dove Marine Laboratory); attached to submerged plates and tests of *Ascidiella aspersa*.

REMARKS

There is no gainsaying the fact that many different species of *Folliculinidae* have been recorded as *Folliculina ampulla* by past workers. A look at Fig. 2 will show that Laackmann's sketches (1910) depict four different species; similarly Stein's figures (1867) of *F. ampulla* show specimens of at least

two species; finally, Müller's sketches (1854) of his smaller specimens (200μ) of *F. ampulla* really depict the separate species *F. simplex* Dons. I have made a thorough search for *F. ampulla* both at Plymouth and at Cullercoats, but have failed to collect a single specimen of this species. Fauré-Fremiet (1936*a*) also states that he could not find them on the Breton coast. I have a strong suspicion that the species *Folliculinopsis ampulla* (multinucleate) is really non-existent. The uninucleate *F. ampulla* of past workers will on examination turn out to be *F. simplex* or *F. viridis*; while the multinucleate forms, named as *F. ampulla* in the past, would probably be *F. andrewsi*, or *F. producta*. However, I leave the abolition of this species to future workers.

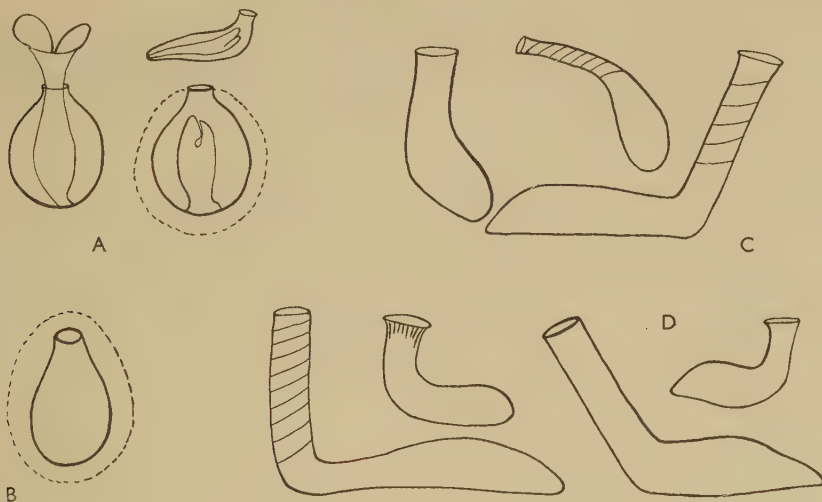


Fig. 2. *Folliculina ampulla* of various authors, some of which may be true *Folliculinopsis ampulla* (Müller). A, *Folliculina ampulla* Müller, the uninucleate small variety, $\times 125$. B, *F. simplex* Dons, as sketched by Dons, to show that it is the same species as that sketched and named *F. ampulla* by Müller, $\times 125$. C, *F. ampulla*: cases as sketched by Stein: there are at least two species represented here, $\times 50$. D, *F. ampulla*: cases as sketched by Laackmann: all four of them appear to belong to different species, $\times 50$.

Genus *FOLLICULINA* Lamarck, 1816

The genus should now be restricted to those forms that show a simple macronucleus and a single case (not divided by a constriction). The genera listed by Kahl (1932, 1933)—*Folliculina*, *Metafolliculina*, *Mirofolliculina*, *Parafolliculina*, *Pseudofolliculina* and *Pebrilla*—were founded by various workers and based mainly on the characters of the case. It has been shown by Fauré-Fremiet (1936*b*) and Das (1947*b*) that the case alone, when considered as a generic or even a specific character, causes endless confusion, if it is not taken in conjunction with other anatomical structures. The present genus *Folliculina*, from which the multinucleate forms have been removed, presents a well-knit group of species, and no useful purpose will be served by splitting

it up further. All the multinucleate forms can be included in *Folliculinopsis*, while the species with a 'double' case (divided into chambers), but simple nucleus, may be put in the genus *Parafolliculina*.

Folliculina simplex Dons (Fig. 3A)

Folliculina ampulla Müller, 1854, *in part*

F. elegans Stein, 1867

F. boltoni Kent, 1882

F. lentus Henneguy, 1884

F. simplex Dons, 1912

DIAGNOSIS

Size and case: very small, maximum about 200μ long; case patulous, rounded or ovoid, with marginal expansions; tube short or absent and without lipped funnel. *Nucleus* simple; rounded in outline, and situated in the proximal half

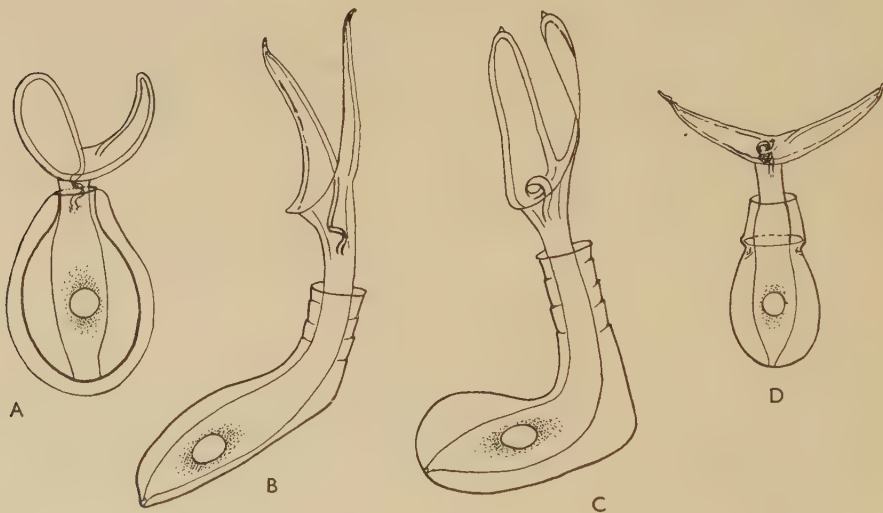


Fig. 3. A, *Folliculina simplex* Dons, $\times 200$. B, *F. elegans* Clap. & Lach., $\times 125$. C, *F. viridis* Wright, $\times 175$. D, *Parafolliculina hirundo* (Kent), $\times 200$.

of the body. *Cell-body* with peduncle absent; body short and cylindrical; attached by a broad base to the case. *Pigment*: body light bluish green generally and bottle-green only about the nucleus. *Ciliary bands*: about twenty-four on body and five on the peristomial lobes. *Peristomial lobes*: short and broad, the two appearing as one bilobed structure; left lobe larger and rounded and right one smaller and narrow throughout. *Larva* cylindrical and elongated, $150 \times 25\mu$; narrowed and truncated anteriorly.

LOCALITY

Cullercoats (Das, 1947*a, b*); attached to tests of *Ciona intestinalis* and to submerged plates in aquarium.

REMARKS

On comparing the figures and descriptions of Müller (1854), Stein (1867), Kent (1882), and Henneguy (1884), it appears that *Folliculina elegans*, *F. boltoni*, and *F. lentus*, are all one and the same species, and that they are identical with *F. simplex* Dons, 1912. As *F. simplex* is the first well-defined species, the later name by Dons is retained.

***Folliculina elegans* Clap. & Lach. (Fig. 3B)**

Folliculina elegans Clap. & Lach., 1858

F. ampulla Laackmann, 1910, *in part*

DIAGNOSIS

Size and case: fairly large, extended animal about 600μ long; case about 450μ ; ampulla 250μ ; tube shorter than ampulla ($150\text{--}200\mu$) and with three turns of the spiral thickening; ampulla lies horizontally on substratum and the tube placed at an angle of about 45° (never 90°); funnel with expanded collar. *Nucleus* simple; ovoid or oblong, situated at basal end of body. *Cell-body* with short thin peduncle; proximal half of extended animal stouter than distal half. *Pigment*: body of light green colour generally; green pigment concentrated around nucleus. *Ciliary bands*: about forty on the body and five to six on the peristomial lobes. *Peristomial lobes*: flat, ribbon-shaped, tapering distally into a sharp tip. *Larva*: elongated, vermiform; $300 \times 50\mu$; oral ciliary disk broad and well-marked; after attachment the larva puts forth a long proboscis-like projection, which helps in making the tube of the case.

LOCALITY

Port Erin (Bruce, 1935); Plymouth (first record); Cullercoats (first record); attached to green algae and *Flustra*.

REMARKS

One must be very careful in distinguishing the three species: *Folliculina elegans* Clap. & Lach., *F. viridis* Wright, and *F. aculeata* Clap. & Lach. All three are uninucleate species, all of them have a comparatively short tube which is never longer than the ampulla, and all have only three spiral turns of the thickening on the tube. Looking at the case, the ampulla of *F. viridis* is the stoutest, although this is the smallest of the three species, and the tube is always shorter in length than the ampulla. The ampulla of *F. elegans* is probably the longest with the tube again shorter than ampulla; while the case of *F. aculeata* is characterized by the ampulla and tube being of about the same length. The peristomial lobes are, however, the main differentiating structures.

In *F. viridis* each lobe is leaf-like, non-acuminate and ends abruptly in a short, sharp tip; in *F. elegans* each lobe is ribbon-shaped, tapering, and ends in a somewhat elongated point; while in *F. aculeata* each lobe is acuminate and ends in an accentuated pointed tip. The three species thus form a progressive evolutionary series, so far as the peristomial lobes are concerned. The colour may be distinctive, but I have always found it difficult to distinguish them merely by colour, as variations are quite common in all three species.

Folliculina viridis Wright (Fig. 3C)

Folliculina ampulla Müller, 1854, *in part*

F. viridis Wright, 1862

F. ampulla Laackmann, 1910, *in part* (one of his sketches)

DIAGNOSIS

Size and case: smaller than *F. elegans*, not more than 400μ when extended; case only 250μ in length; tube a little more than half the length of the stout quadrangular ampulla, and usually at right angles to it. *Nucleus* simple; large, ovoid, and situated at about middle of ampulla. *Cell-body* stout in the middle and tapering at both ends; peduncle short and narrow. *Pigment*: yellow-green colour (yellow predominating); pigment more concentrated around nucleus. *Ciliary bands*: about fifty on the body, and five to six on the peristomial lobes. *Peristomial lobes* flat, leaf-like, with tips rounded; each lobe terminates abruptly in a sharp point of ectoplasm. *Larva* elongated, vermiform, about $200 \times 40\mu$; colour yellowish with yellow-green pigment concentrated near the oral ciliary disk; as in *F. elegans* the larva after attachment puts forth a long proboscis-like projection.

LOCALITY

Swansea (Fowell, 1944); Plymouth (first record); Cullercoats (first record). Attached to various green algae.

REMARKS

F. viridis can be easily confused with *F. elegans*; but, as mentioned by Das (1947b), the smaller size, yellow-green colour, erect tube, quadrangular ampulla, and non-acuminate peristomial lobes, should suffice to distinguish it from *F. elegans*.

Genus **PARAFOLLICULINA** Dons, 1914

Parafolliculina hirundo (Kent) (Fig. 3D)

Folliculina hirundo Kent, 1882

DIAGNOSIS

Size and case: very small size, about 180μ when extended; case horizontal and 130μ long; annular constriction at base of free end of the case (i.e. a short chamber, the neck, is present). *Nucleus* simple; ovoidal, situated at about the

middle of the cell-body. *Cell-body* short and cylindrical; peduncle absent, attachment by a broad base. *Pigment*: very feebly coloured; bluish green; colour somewhat dark around nucleus. *Ciliary bands*: about twenty on the body and five on the peristomial lobes. *Peristomial lobes* narrow, tapering, nearly symmetrical and lying far apart, so as to create the impression of a single flat T-shaped structure. *Larva*: resembles that of *F. simplex*, except that it is broadly rounded anteriorly.

LOCALITY

Channel Islands (Kent, 1882).

REMARKS

I have not been able to find specimens of this species either at Plymouth or at Cullercoats. It is common on the Breton coast of France and should occur on the south coast of England. The distinctive collar-like band at the free end of the case, and the symmetrical peristomial lobes should immediately distinguish it from the similar *F. simplex*.

KEY TO BRITISH FOLLICULINIDAE

(After Das, 1947*b*)

Macronucleus consisting of a string of beads

Tube not longer than ampulla

Folliculinopsis ampulla (Müller)

Tube longer than ampulla and spirally ridged

Tube with five to eight spirals; maximum size of animal 1000 μ ; peristomial lobes a little shorter than tube.

F. andrewsi (Hadži)

Tube with eight to fourteen spirals; maximum size 1500 μ ; peristomial lobes about half as long as tube.

F. producta (Wright)

Tube with eighteen to thirty spirals; maximum size up to 3000 μ ; peristomial lobes less than one-third the tube.

F. elongata n.sp.

Macronucleus simple

Case divided by annular constriction

Parafolliculina hirundo (Kent)

Case entire, not constricted

Tube absent; maximum size 200 μ ; peristomial lobes asymmetrical, short and broad.

Folliculina simplex Dons

Tube shorter than ampulla, with three spirals, and at 135° to ampulla; maximum size 600 μ ; peristomial lobes tapering.

F. elegans Clap. & Lach.

Tube shorter than ampulla, but at 90° to it; maximum size 400 μ ; peristomial lobes rounded at tip.

F. viridis Wright

ACKNOWLEDGEMENTS

I am greatly indebted to Prof. A. D. Hobson, F.R.S.E., Director, Dove Marine Laboratory, Cullercoats, for giving me facilities for work in the laboratory during 1946-47 and for constant help and criticism. To Mr F. S. Russell, F.R.S., Director, Plymouth Laboratory, I am sincerely grateful for allowing me a table at the Laboratory and access to the library.

SUMMARY

A brief résumé is given of the work done on British Folliculinidae up to the present time.

Descriptions follow of eight British species, many of which are revised accounts based on personal observations.

A new species, *Folliculinopsis elongata*, is described.

A revised key for the identification of British Folliculinidae is given.

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THE DECLINE OF *ZOSTERA MARINA* L. AT SALCOMBE AND ITS EFFECTS ON THE SHORE

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(Plates I-IV and Text-fig. 1)

The history of the almost total disappearance of the eel-grass, *Zostera marina* L., from the Atlantic coasts of North America and a little later along the Atlantic coasts of Europe, in the early 1930's, is fairly well known (for references see Butcher, 1934 and Tutin, 1938, 1942), though the cause has never been satisfactorily determined. The symptoms of the 'wasting disease', with which it was stricken, are brown spots on the leaves which spread and darken until much of the leaf is covered, the leaf then becoming detached from the plant. Of the variety of factors to which this destruction of the living green tissues has been attributed a fungus, *Ophiobolus halimus* Mounce & Diehl (Mounce & Diehl, 1934; Petersen, 1935), and a species of *Labyrinthula* (Renn, 1936; Young, 1943) both rank high in probability as the chief causative agents. Atkins (1938) has strongly criticized the suggestion by Tutin (1938) that the fundamental cause of the epidemic was lack of sunshine in 1931-32 which led to enfeeblement of the plant with a lowering of its resistance to the parasites.

In the Plymouth district and at Salcombe a weakening of the growth of *Zostera* (locally known as 'gravit') was first noticed in the spring of 1932. During the summer of that year very little *Zostera* could be obtained, and that consisted of short pieces. Blackening and rotting at the ends of the leaves was usual. At Salcombe there was a slight growth during the early autumn but it did not result in restoring the beds, or banks, to their old condition and it died down during the following winter. By early 1933 the *Zostera* banks at Salcombe were almost entirely devoid of green leaves and presented a blackish appearance, though here and there were small green patches due to a sparse growth of a few plants with leaves about a foot long. A few of these leaves, however, showed blackened and slightly rotted tips, for they still had the disease. These growing plants were situated at the edges of the old banks and seemed to be colonizing new areas of sand. The years that have passed since then have seen little or no extension of these patches, which for a time became even further reduced. Their present extent is discussed below.

Soon after the disease had reached Salcombe the appearance of the shore at the lowest levels exposed by spring tides was markedly changed. In the late 1920's the mud flats north of the town, and the sandy muddy flats on each side

of the harbour between the ferry and the rocks at the seaward end near Biddlehead and Fort Charles (see Text-fig. 1), were green at low-water spring tides, so thickly did the *Zostera* cover them. Now there is little to be seen except grey mud above the town and shingly muddy sand and some seaweed below the ferry, for algae occupy some positions formerly covered with *Zostera*, especially on the south-east side between Small's Cove and Mill Bay, the area I know best of all. It is about this region of the harbour that I am here chiefly concerned, for I have followed its changes year by year, with the students' classes in the spring and when collecting polychaetes in the summer. Memory and notes are aided by old photographs; the latter are especially valuable in bringing to light changes in level which might otherwise have gone almost unnoticed. It seems well to publish some record of these changes whilst memories of past events are still fairly vivid, especially as the younger workers of to-day are almost unaware of the conditions that prevailed at Salcombe nearly twenty years ago.

The fauna of Salcombe was thoroughly investigated at the beginning of the present century by Allen & Todd (1900). Much of this account still holds good: the rocks, the Salstone region, indeed any of the areas where *Zostera* did not flourish are not very different to-day than they were then. The *Zostera* areas were also much the same until 1931; after that, with the death of so many of the plants, changes set in. The first animals to become scarce were those whose habitat was the leaves of the *Zostera* itself; such species as *Rissoa membranacea* (J. Adams), *Cantharidus striatus* (L.) and *Haliclystus auricula* (Rathke). Some of these seemed to disappear entirely, for they have not, so far as is known, been taken in this locality since. For a time the roots and rhizomes, though dead, still bound the sand in the raised mounds so characteristic of *Zostera* beds. Even as late as 1935, when there was very little living *Zostera* to be seen, the mounds or banks were still more or less unchanged and the buried fauna revealed by digging was much as before. The eventual decay of the roots and rhizomes, which in the later stages were often dug up in a soft and blackened condition, loosened the sand and the tidal currents flattened the mounds and washed them away. The level of the shore fell and in some places the substratum became much more stony through a concentration of stones which had previously been much diluted with, or covered by, sand. Thus the character of the substratum was changed, making it less suitable for some species and more suitable for others, and certainly making it much harder to dig into. These changes in fauna and flora will be discussed later.

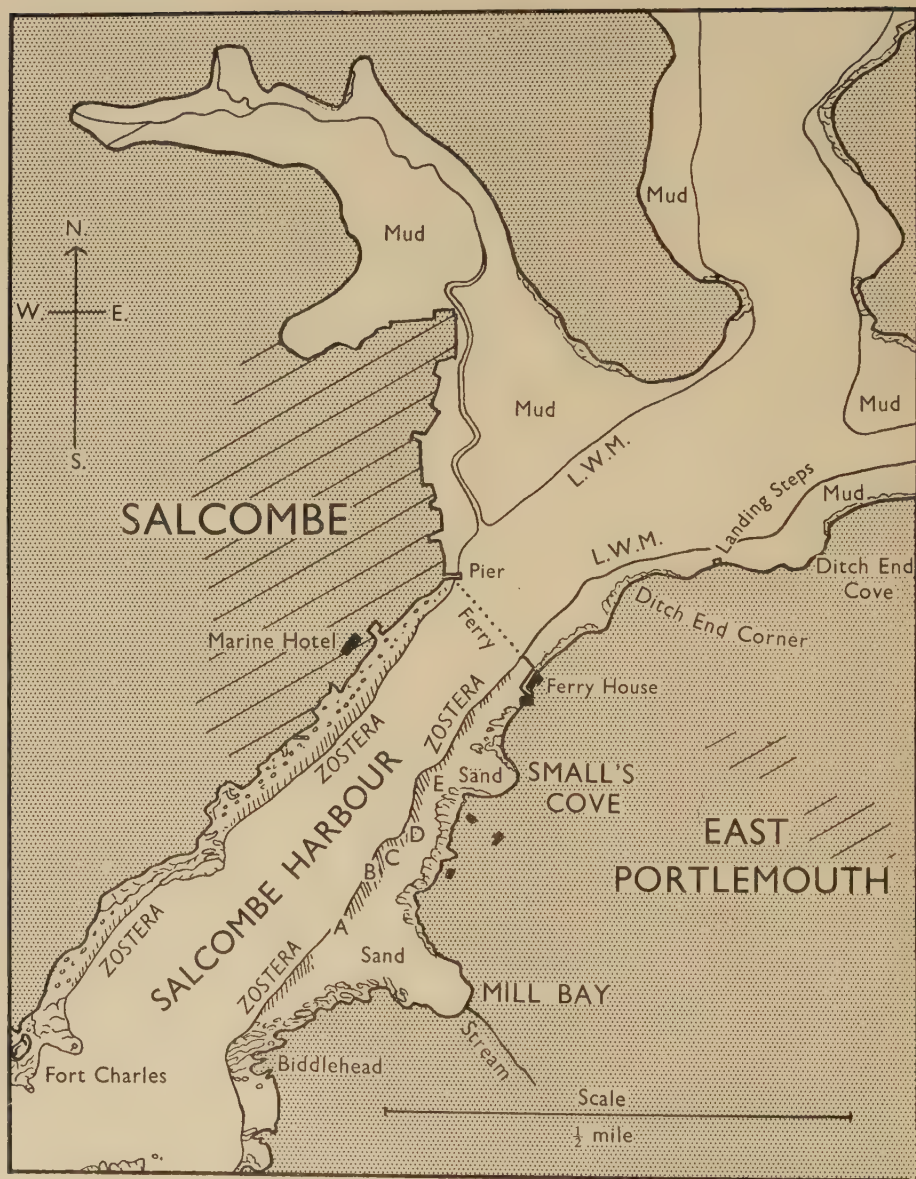
THE DISAPPEARANCE OF BANKS NEAR LOW-WATER MARK

Much of the following argument is based on comparisons of photographs taken on various dates at, or about, low water. It is necessary in making the comparisons to know fairly closely the actual heights with reference to chart

datum of the water levels depicted. The level of low water can be obtained in the first place from the Admiralty Tide Table predictions, using those for Devonport, the nearest port for which predictions are available. The actual observed height of a tide, however, frequently does not coincide with the prediction, and I am therefore grateful to the Hydrographer to the Navy and his Department for supplying the necessary corrections for the tides referred to in this paper. The corrections for the 1926 and 1935 tides are based on comparison between observations and predictions at Devonport, but for the 1947 and 1948 tides by comparison between observations and predictions at Newlyn. It is assumed that the Newlyn corrections apply closely to Devonport, the tidal range being very similar at both ports. It is assumed also that the tides at Salcombe follow the Devonport tides closely; the tidal range at Salcombe is very similar to that at Devonport. Thus the corrected levels for Devonport are here used to compare the water levels recorded in the photographs on the different dates. Throughout the paper all datum references are to Devonport. In the enclosed harbour of Salcombe the strength and direction of the wind probably has a greater influence on the water level than at Devonport, and therefore the weather at the time the photographs were taken is considered here. Whilst it is realized that this and other factors introduce some uncertainty into the comparison between water levels on different dates it is not believed that the main conclusions are substantially affected.

The photographs reproduced in Pl. I should now be examined. Fig. 1 gives a general view of the decaying *Zostera* banks looking north-east from Mill Bay on 18 July 1935 from approximately the position marked A in Text-fig. 1. It must have been taken at or about low water, though the actual time was not recorded. On that date the Admiralty Tide Table predicted a low tide of 0.0 ft., Admiralty chart datum, at Devonport, but observation showed that it was 1.0 ft. higher. In the photograph the ripples on the water and the direction in which the seagull faces both suggest a south-westerly breeze and this seems to be confirmed by the meteorological report for that day which records at Plymouth a south-west by west wind of Force 4 at 13.00 hr. G.M.T. At Salcombe such a wind would blow up the estuary, not down it. This breeze would tend to hold back the water draining from the estuary, thereby preventing the tide from falling to quite such a low level as it otherwise would have done. It is assumed, therefore, that at the time the photograph was obtained the water level was not less than 1 ft. above chart datum.

Fig. 2 is a photograph taken on 26 March 1948 from a position which is identical, or almost identical, with that from which fig. 1 was taken. This position for the second picture was obtained by careful sighting of landmarks shown in the first one. These are: first, the mast, chimneys and roofs of the buildings near the ferry landing, seen in the middle distance to the left centre of the picture, and the manner in which they align with the hedges of the fields on the hillside far behind them; secondly the alignment of a chimney on the



Text-fig. 1. Sketch-map of Salcombe harbour and vicinity showing very approximately positions of *Zostera* beds (close hatched) on both sides below the ferry as they existed about 1926. *Zostera* also grew on the lower levels of the exposed mud above the ferry, but as the extent of the areas it covered is more doubtful they are not indicated. A, B, etc. mark the approximate positions from which the photographs reproduced in Pls. I-IV were taken, the camera always facing the Ferry House. A, Pl. I, figs. 1, 2; B, Pl. II, fig. 1; C, Pl. II, fig. 2; D, Pl. IV; E, Pl. III, figs. 1, 2.

lower of the two houses on the right with a corner and chimney of the house above and behind. These landmarks fix the position to within a yard, as was determined at the time the second photograph was obtained. On that occasion the distant hillside was slightly obscured by mist and hence is not so clearly rendered in the second photograph as in the first.

On 26 March 1948 the predicted low-water level was 1.9 ft. *below* datum at Devonport. However, observation at Newlyn showed that there the tide was 2.5 ft. higher than the prediction. If we apply an equal correction to the Devonport prediction we assume that the level there was actually 0.6 ft. *above* datum. From this we can further assume that the Salcombe low water on that day was 0.4 ft. below low water of 18 July 1935 and that there is at least this difference in the level of the water shown in the photographs, for whilst that of 26 March 1948 was taken at dead low water that of 18 July 1935 may have been taken a little before or after. However, on 26 March 1948 a fresh breeze blew down the estuary towards the open sea; at Plymouth an east wind of Force 4 was recorded at 12.00 hr. G.M.T., an hour before low water at Salcombe. By 18.00 hr. G.M.T. the wind had increased to Force 5. This wind at Salcombe would have aided the outflowing tide and tended to depress, not raise, the level. At Newlyn the same wind (the Lizard record also shows an east wind of Force 4 at 12.00 hr. G.M.T.) would not have this effect but rather the reverse.

Certainly at Salcombe the tide exposed ground not often uncovered, and in the opinion of the local ferry men made 'a big out', an opinion with which our experienced collector, Mr William Searle, concurred. Thus in accepting the Newlyn correction as being applicable to Salcombe on this particular day we are more likely to be overcorrecting than otherwise, and it therefore seems reasonable to assume that the level of the water shown in Pl. I, fig. 2 is not only lower than that shown in fig. 1, but is likely to be at least 6 in. lower and may well be lower still. If, for the purpose of what follows, this figure of 6 in. is taken, any estimated differences in ground level based on it can be regarded as minimal.

With these facts in mind the photographs may be compared. In the July 1935 picture there is in the near distance a low mound whose seaward edge slopes fairly steeply down to the main channel. This mound of sand, bound by dead roots and rhizomes of *Zostera*, stretches into the distance beyond the left-hand boat stranded on top of it and as far as the figure in a white jersey. The steepness of the seaward slope can be judged by the bathers waist deep within a few yards of the edge and by the boat being rowed close inshore. (Details of bathers, oars of boat, etc., which are clearly visible in the original print, may not be discernible in the reproduction.) Very little living *Zostera* is to be seen, but the position chosen for this photograph includes a few plants in the foreground. A few also still grew in small patches here and there on the mound, whose greater area was, however, bare. It may be noted now that at no time did the *Zostera* completely disappear, a little always being present—this matter will be considered later on.

The photograph of March 1948 shows a very different state of affairs. Where the mound previously existed there is now only water. The whole of the sandy foreground in Fig. 1 has been washed away and the change is strikingly evident if a comparison be made of the conditions around the site of the cross marked on each photograph to indicate the position from which the photograph reproduced in Pl. II, fig. 2, was taken a few minutes earlier. The water covering the site of the former mound was about a foot deep, in some places deeper, and this, it should be remembered, with what was almost certainly a lower tide; the general ground level must therefore be lower by 2 ft., perhaps even 3 ft. The 1935 photograph was taken from a tripod set on sandy ground above water level, whereas to obtain the 1948 photograph from the same position I was forced to wade almost up to the knees in water, again a difference in ground level of 2 or 3 ft. The slope to the main channel in 1948 is irregular but on the whole less sudden and steep than in 1935, at least at the water's edge, for it deepens again farther out. Collectors of to-day have less ground to work over than in 1935, and it needs a lower tide than before to get on to what is left.

A few words of explanation about the piles which appear in the 1948 picture are needed. They formed the seaward extension of a repair base for damaged landing craft which was built in Mill Bay by United States forces during the war. Apparently the craft were brought in between the two groups of piles and hauled up a slipway the lower end of which may be seen as a dark line on the right of the photograph. The base occupied a portion of the north-east side of Mill Bay; it is now derelict, an ugly eyesore in a lovely setting. There is no reason to suppose that the existence of this base has had any material effect on the sandbanks of the lower levels, changes in which were very marked before the Americans came. Moreover, these changes have occurred over a very much wider area than that affected by the activities of the base.

So far, levels in 1935 have been compared with levels in March 1948, but it is possible to go back another nine years. When in March 1926 a class in marine biology conducted by Dr (now Prof.) J. H. Orton at Plymouth was taken one day to Salcombe, I obtained the photograph reproduced in Pl. II, fig. 1. The collectors are busy on the steep seaward edge of a *Zostera* bed in the heyday of its development. The thick covering of plants is clearly seen and it should be remembered that the growth would be thicker still in the summer. The steep slope at the seaward edge is even more strongly marked than in the 1935 photograph when the beds were already beginning to disintegrate. This steep slope is very evident on the well-developed beds in the middle distance as well as in the foreground, in spite of the poor quality of the camera lens whose definition at the sides and in the distance left much to be desired. Nevertheless, landmarks are sufficiently clear for the camera position to be determined, and on 26 March 1948 an attempt was made to reach the same viewpoint (B in Text-fig. 1). The landmarks used were the same or similar to

those already described during the comparison of the photographs in Pl. I. The mast and buildings near the ferry landing and their parallax with the hedges of the hillside behind them fixed the position in one direction, whilst the tall white mast on the right and the gable of the house close by gave another. It is true that the gable in the 1926 photograph is partly obscured by trees since cut down but its position can be made out. As it happened, however, I was unable to reach the proper position, for after wading half-way up to the knees in water at the lowest ebb of the tide the ground began to drop away fairly steeply and I was unable to get out farther without flooding my rubber knee-high boots. I judged that in the true position I should be well over the knees in water and the camera held at eye-level would have been lower than the waist-level camera of 1926. Thus the photograph reproduced in Pl. II, fig. 2 was actually taken several feet landward of the 1926 position and closer, along the same straight line, to the house and flag-pole on the right (position c in Text-fig. 1). This landward position has resulted in the amount of shore exposed in the middle distance being apparently greater in 1948 than in 1926, but a consideration of the difference in viewpoints will show that this idea is erroneous. The viewpoint of 1948 must have been close to the cross marked on the 1926 photograph, and this same viewpoint is marked, as we have already seen, on the photographs in Pl. I. Actually the seaward edge of the shore at low-water mark extreme spring tides is not very much changed for the area shown in Pl. II, fig. 2, though it is a little nearer the land on the whole than before, but the ground is lower and it takes a lower tide to uncover it than it did. It is this part of the shore that is so much more stony than it was years ago. The large *Zostera* bank in the foreground of the 1926 photograph has completely disappeared and the level here must have dropped 2 or 3 ft. This bed in dead and dying condition was still in existence in 1935, for it was none other than the low mound in the near distance seen in Pl. I, fig. 1. That this is so is immediately apparent when it is remembered that the cross on that photograph and the cross on Pl. II, fig. 1, both indicate the same position as closely as can now be determined.

So far the tidal level of the 1926 photograph has not been considered. The picture most probably was obtained on 16 March for which the tidal prediction was 1.7 ft. *below* datum, but the observed height at Devonport was actually only 0.7 ft. *below* datum. The prediction for the previous day's tide had been a little lower but the class on that day was definitely not at Salcombe. No other tide in March 1926 was predicted as low or lower than that on 16th. For that day the weather report records a light westerly breeze of Force 2 and it will be seen that the water in the picture is but lightly rippled. This breeze would scarcely affect the water level which can, therefore, be assumed to have been about a foot lower than that seen in the 26 March 1948 photographs (Pl. I, fig. 2, and Pl. II, fig. 2—but see remark concerning this day's wind, on p. 399), and was lower than in the photograph taken in July 1935 (Pl. I, fig. 1).

The extensive *Zostera* banks which previously existed on the west side of the harbour, under the Marine Hotel and extending towards the harbour mouth, have similarly disappeared, and only a few sparse patches of *Zostera* remain. These banks were much more muddy than those on the east side and there were variations in the fauna to correspond. My visits to the west side have been less frequent than to the eastern shore and no photographs showing past conditions have been traced. Mr William Searle ('Bill'), the Laboratory's veteran collector, who has regularly worked under the Marine Hotel, informs me that the ground where the *Zostera* banks formerly existed is more stony and more difficult to dig into than the banks themselves used to be, and there is no longer a seaward edge where the ground suddenly sloped steeply downwards. To-day the collecting ground is uncovered by the tide for a shorter period than before, and with the tide at its lowest the water's edge is closer inshore.

It seems certain that the *Zostera* beds on this western side, south of the Marine Hotel, were considerably broader than indicated on the sketch map (Text-fig. 1), extending out beyond low water spring tides, as they do to-day.

THE ACCUMULATION OF SAND NEAR HIGH-WATER MARK

A consideration of four photographs has shown that the ground near low-water mark, on the east shore, has been lowered 2 ft. or more since most of the *Zostera* died, and the question now arises as to what has become of the sand which has been washed away. This question is answered, apparently, by a comparison of two more photographs which will now be considered.

The photograph of the north-west corner of Small's Cove reproduced in Pl. III, fig. 1, was taken in 1926 on the same day as that in Pl. II, fig. 1. On 21 May 1947 the photograph shown in Pl. III, fig. 2, was taken from the same viewpoint (E in Text-fig. 1), obtained by getting the lower left-hand buildings by the ferry slip in the same alignment with the distant hillside as shown in the earlier photograph. It was found that a very small displacement was sufficient to give appreciable parallax, and it can therefore be asserted with confidence that the camera in 1947 occupied a position in space almost identical with that of the camera of 1926, and that any variation could not have exceeded more than a few inches in any direction. The 1947 photograph was taken $1\frac{1}{2}$ hr. before low water; the tide when the 1926 photograph was obtained seems to have been a little lower. Differences in definition between the photographs are due partly to different atmospheric conditions and to the much better lens used in 1947.

Two features shown by the photographs call for first comment. The high jetty seen at the ferry landing in 1947 was not in existence in 1926. The end section of the drain pipe, so conspicuous in 1926, was accidentally broken off at a later date but the remainder of the pipe, which I am assured has not been repaired or rebuilt, had by 1947 disappeared under a covering of sand and it is still so buried to-day. The natural rocks, however, show most clearly the rise

in sand level, for it is plainly evident that in 1947 the sand was much more banked up at the foot of the cliff than in 1926, especially on the right towards high-water mark, the rise being some 3 or 4 ft. In the 1926 photograph high-water mark spring tides is out of sight beyond the right-hand edge of the picture, but in the 1947 photograph a thin dark line of stranded weed stretches from the right-hand edge to the cliff rocks near the centre of the picture and marks the highest level reached by the previous high tide, a moderately high spring. The tongue of dark fucus-covered rocks near half-tide mark in the middle distance was more submerged by sand in 1947 than in 1926 and it is obvious that the sand beyond them, towards the ferry house, had also been banked up. At the top of this little bay, out of sight beyond the right-hand edge of these photographs, sand has been steadily accumulating year by year, raising the height of the beach near high-water mark, until an appreciable area is no longer inundated by spring tides. At that place I have watched with interest the slow but steady formation of a small sand dune colonized by *Honckenya peploides* Ehrb. and maritime grasses (*Festuca*, *Agropyrum*). The sand level is much the same to-day (December 1948) as it was in May 1947.

Sand has also accumulated in the upper part of the larger Mill Bay, but of this I have no definite records of my own. I am much indebted, however, to local inhabitants for various information, particularly to Mr and Mrs R. C. Tyler who, since 1916, have occupied the house next to the ferry landing on the East Portlemouth side, and to Mr Harry Cook and son, boatmen of Salcombe. They all agree that sand began to accumulate on the east side of the harbour at least as early as 1920, long before there was any reduction in the growth of the *Zostera*. This accumulation steadily increased and still goes on. Material washed and blown up from the old *Zostera* mounds therefore does not by itself fully account for the banking up of the sand on the higher shore levels; it has merely added to a process due to other causes. These causes lie outside the scope of the present paper, but it is worth recording that Salcombe was formerly much visited by sailing vessels which took away from Mill Bay large quantities of sand for ballast. Sand for building purposes was also removed in barges to Kingsbridge; according to Mr Harry Cook hardly a day went by without one or more barges visiting Mill Bay for this purpose. During the early years of the present century this traffic decreased and the last barge load for Kingsbridge was taken, so I am informed, shortly after the end of the 1914-18 war. About this time the high tide reached a wall by the roadway at the inner end of Mill Bay; but to-day this wall is silted over and the high-tide mark is about half-way down the bay.

The removal of so much sand in years gone by must have kept the level down—assuming that sand was accumulating all the time—and it seems therefore reasonable to suppose that the present silting may in some measure be due to the cessation of these activities. It should be noted that at the time this sand was being taken there were extensive *Zostera* beds on both sides of

the harbour; some description of these will be found in Allen & Todd (1900).

On the eastern shore the sand in general drifts to the north-east (prevailing winds come from points between south and north-west), and at the present time is piling up, especially on the rocks at Ditch End Corner, north-east of the ferry. It has turned the corner and has already travelled along the south shore as far as the old steamer landing steps just west of Ditch End Cove, covering muddy shingle and rocks.

It should be noted that in this sheltered harbour really big waves are not generated and the great transport of sand from one locality to another, such as is of common occurrence during stormy weather on exposed beaches like those of north Cornwall, is unlikely to take place. However, Mr Tyler told me that in a gale the sand banked up against the sea wall by the ferry house is sometimes washed away but it always comes back again, often on the next tide.

The sand slopes steeply down from high-water mark for most of the tidal range. It is loose, well drained and devoid of any obvious buried fauna. At the bottom of the slope the ground levels off, and in the firmer and wetter sand *Arenicola*, *Lanice* and other members of a normal sand fauna appear.

THE EFFECT ON THE FAUNA

The death of the *Zostera*, and the consequent modification of the physical character of the areas it occupied, have had a noticeable effect on the fauna and flora. This has been most marked between Small's Cove and Mill Bay where the washing away of the sand has produced a stony ground with many of the stones exposed on the surface. This stony ground occupies a position where the most landward extensions of the *Zostera* lay; part indeed may not have been covered by *Zostera* at all. The stones give attachment to several species of algae, particularly *Enteromorpha* sp., *Ulva* sp., *Fucus serratus* Linn., *Laminaria saccharina* Lamour., and species of *Ectocarpus*, *Ceramium*, *Polysiphonia*, etc. Previously there had been growths of these seaweeds on a number of large stones which were scattered here and there, especially on this landward side of the *Zostera* beds, but the growths were nothing like as abundant as they are now. The photograph reproduced in Pl. IV shows the present seaweed-covered stony area very well. It was taken on 21 May 1947, 15–20 min. after dead low water when the tide had risen 2–3 in., as can be determined from another photograph, not reproduced, which gives a closer view of part of the same region at dead low water. The Admiralty Tide Table prediction for that day gives low tide as being 0.7 ft. *below* datum, but the observed height at Newlyn was 2.0 ft. *above* the prediction, from which we conclude that the water level when the exposure was made would be about 1.5 ft. *above* datum. There was no wind. The viewpoint for this picture is indicated, approximately, by the cross on Pl. II, fig. 2 (when the tide was lower) and at D in Text-fig. 1. The

view includes the only *Zostera* bed visible on that day; on the picture a dotted line has been drawn around it. The *Zostera* extended a little way under water at the lowest ebb of the tide. In 1948, conditions were still much the same as when this picture was obtained.

The extension of algal cover has very likely brought about an increase of animal life normally associated with stones and seaweed (e.g. *Littorina littorea* (L.), *L. littoralis* (L.), etc.), but no comparable figures exist and the surface fauna of this area has not been specially investigated. It appears to be much as would be expected in such a situation and it certainly lacks the interest of the specialized buried fauna for which this part of the Salcombe estuary has long been noteworthy. This is, of course, the remarkable and seemingly unmatched concentration of commensal animals in the ground on both sides of the harbour.

At the bottom of the slope down from Small's Cove there is still a large colony of *Lanice conchilega* (Pallas) and an abundance of *Arenicola marina* L. In the galleries of some of the *Arenicola* fairly large specimens of *Harmothoe lunulata* var. *marphysae* McIntosh may be found. Part of this area is uncovered in the near distance in Pl. III, fig. 1. *Zostera* beds occupied the lower levels of this cove and stretched in a nearly continuous bank to Mill Bay¹ and beyond (see Text-fig. 1 and Pl. II, fig. 1). It was in this bank that *Acrocnida brachiata* (Montagu), with its commensals *Mysella bidentata* (Montagu) and small specimens of *Harmothoe lunulata* var. *marphysae*, were abundant. The brittle-star is still common in the stony soil, but is not as numerous as formerly and seems less frequently accompanied by its commensals which, since the war, have been appreciably more difficult to find with it. This may, of course, be merely a passing phase, but it seems hardly likely that the brittle-star will again reach its former abundance in ground less suitable for it. The ground itself is relatively barren and but few animals of any kind are found for much hard digging, for there has taken place a very marked diminution in the number of species and individuals turned up by the fork. Thus *Phascolosoma elongatum* Keferstein, with which was often *Mysella bidentata*, was formerly common but is now infrequently found, while *Amphitrite edwardsi* Quatrefages with its large handsome commensal *Lepidasthenia argus* Hodgson have become very rare. These two associated polychaetes were not uncommon, although always less numerous here than in the muddier opposite shore of the harbour where they are also less abundant than before. The synaptids, *Leptosynapta inhaerens* (O. F. Müller) and *Labidoplax digitata* (Montagu), and their commensals, were previously present in small numbers on the Mill Bay side but are now rarely turned up when digging, and the same remark applies to *Upogebia deltaura* Leach and *U. stellata* (Montagu), while *Lepton squamosum* (Montagu), an inhabitant of

¹ The gap in the bed opposite Mill Bay, indicated in Text-fig. 1, is seen in photographs taken in 1926, and it forms the immediate foreground in Pl. I, fig. 1. It may have been caused by the freshwater stream which ran down the beach and at low tide discharged through it.

their burrows, has not been obtained here for several years. *Callianassa subterranea* (Montagu), always uncommon, is less frequently found than formerly, and this is true also of a number of other non-commensal species such as *Owenia fusiformis* Delle Chiaje and *Notomastus latericeus* Sars.

Towards Mill Bay, where there are still patches of sand with but few stones, *Echinocardium cordatum* (Pennant) and its commensal *Montacuta ferruginosa* (Montagu) are as common as ever, and some other inhabitants of clean sand such as *Caesicirrus neglectus* Arwidsson and one or two species of *Magelona* are also abundant. These species were always to be found here in the sand where *Zostera* did not grow, as well as occasionally in the beds themselves.

In this account no attempt is made to give a complete description of the buried fauna of the area under review, rather is it the intention to record the more obvious changes, or absence of change. The region is still of very considerable interest, but much of its former richness and diversity has been lost and this can be directly attributed to the physical changes following the disappearance of the *Zostera*. In my opinion overcollecting is not the cause. It would have been possible to overcollect on this shore but care was taken that this should not happen. During the war very little collecting was done¹ (there were no students' classes at Plymouth during the years 1941-45 inclusive), but the fauna has shown no sign of recuperation, for, on the contrary, it was definitely poorer after the war than before. It has become more than ever necessary to avoid excessive digging over the smaller area now uncovered and it is sincerely to be hoped that future collectors will do their utmost to conserve what remains.

THE SURVIVING *ZOSTERA*

There remains for consideration the *Zostera* itself. Of the three British species of *Zostera* there is only one likely to be confused with *Z. marina*. This is *Z. Hornemanniana* Tutin, which can grow from half-tide mark down to 1-2 fathoms and it has been seen at Salcombe (Tutin, 1936). The species is distinguished by the smaller stigmas relative to the length of the style and by the smaller seed (Tutin, 1938). It was thought necessary, therefore, to determine the species of the *Zostera* still growing in small quantity at Salcombe.

On 19 July 1947, during the flowering season, my wife aided me in going over all the *Zostera* we could find. On that day the small *Zostera* bed seen in the photograph on Pl. IV was not uncovered, the shallowest part being submerged by a few inches of water and most of it was covered by 6-9 in. at the lowest ebb. Between us we managed to cover most of the ground and obtain flowers and seeds. Without exception the plants proved to be *Z. marina* L.

Although the specific identity of the *Zostera* at Salcombe is the same now

¹ A local informant tells me that Americans stationed at the repair base in Mill Bay collected for eating all the *Ensis* they could find. These were always most numerous near the south-west corner of Mill Bay. *Ensis* was certainly very scarce at that place in 1946 and 1947 but by 1948 small ones were again fairly plentiful.

as it was always supposed to have been, I have a strong impression that present-day plants are shorter and a little narrower in the leaf than they used to be, and that they do not show as vigorous a growth. In this I am supported by the local people whose names have already been mentioned. It seems to be generally agreed that in the summer a length of 5 or 6 ft. was quite usual, though all plants did not attain these dimensions and they were longer in some parts of the estuary than in others. In July 1947 the tallest plants my wife and I could find did not exceed 3 ft. (about 90 cm.) and most were considerably shorter. The breadth of their leaves was $\frac{1}{4}$ in. and less (approx. 5–7 mm.) and the colour a good bright green. On the longer leaves some epiphytic red algae were growing, as is usual; we did not see any *Haliclystus*. In the previous May the plants had been less than 2 ft. long (about 60 cm.) and they had certainly not been longer than this in March. In March 1948 the tallest plants were only 18 in. (about 46 cm.) My memory assigns a length in March and April of 2–3 ft. to the longest leaves and Mr William Searle agrees with this. Prof. J. H. Orton writes 'my impression is that they might have been two feet about'. This would make them one and a half times or even twice their present length for that time of year. The plants in the photograph of March 1926 (Pl. II, fig. 1) look to have been of moderate length, and the appearance suggests that a good many exceeded the 18 in. maximum of March 1948, though the definition is too poor for certainty on this point. Some photographs taken at low tide near Ditch End Cove in 1927 show quite distinctly that the plants there growing on sticky mud were only about 9 in. (or 23 cm.) long, estimated with reference to a collecting basket also in the pictures. The time of year when they were taken is uncertain, but various indications point to January or February as the most likely months. There seems to be no *Zostera* at Ditch End now, and it was probably always shorter there than in the harbour below the ferry. There is, too, the possibility that it was *Z. Hornemanniana* (Tutin, 1942), which seems to grow best on a soft mud substratum, a possibility that is increased when the widths of the leaves, seen in the photographs, are compared with the wicker-work of the collecting basket. The same type and make of basket is still in use and the thin canes of which it is woven have an average diameter of 3.5 mm. with a variation either way of 0.5 mm. The basket in the photographs has an almost identical number of strands and the same general dimensions as present-day ones, therefore its canes must have been of similar cross-section. Now the *Zostera* leaves appear distinctly narrower than the cane strands, and such measurements as are possible on the photograph confirm this impression. One of the characters of *Z. Hornemanniana* is that its leaves are only about 2 mm. broad; those of *Z. marina* are mainly 5–10 mm. broad (Tutin, 1942), although there is said to be a very narrow-leaved variety, *Z. marina* var. *stenophylla* Asch. & Graebn. about which little definite information is available. In the photograph of the *Zostera* bed in Pl. II, fig. 1, the leaves seem distinctly broader than the woven strands of the baskets, thus agreeing with normal *Z. marina*.

If we accept a length of 2 or 3 ft. as the former length for *Zostera marina* in the Mill Bay region in March, it follows that a summer length of 5 or 6 ft. might very well have been attained. Summer *Zostera* obtained near Plymouth when trawling for pipe-fishes in the estuary of the River Yealm or in Cawsand Bay must have reached this length. It was the usual practice to tie bunches of this *Zostera* to stones which were then dropped into the pipe-fish tank in the aquarium. The tank is 3 ft. 4 in. deep, and I well remember how most of the leaves reached the surface and spread out floating horizontally for a foot or more, and this after some of the older and longer leaves most heavily covered with epiphytes had been removed. The *Zostera* in the River Yealm to-day is nothing like that length; there has been very little at all in Cawsand Bay for years, and what is there is short.

Whilst from the above considerations it seems quite definite that much of the *Z. marina* existing before the disease appeared had considerably longer leaves than any of the plants now living in the Plymouth district, it is more difficult to establish that the leaves were also wider. Most of those who remember the plants prior to 1930, and whom I have questioned, agree that the leaves were wider than any seen at present and it has already been stated that that is my own impression. Some equally good observers, however, are not so certain. In the absence of specimens (I have not been able to trace any in herbaria¹) it is impossible to establish the truth, and the only photograph showing the leaves at all clearly is an old picture of pipe-fishes in one of the aquarium tanks among *Zostera* which had almost certainly come from the River Yealm. This photograph, made before 1931, is reproduced elsewhere (Wilson, 1935, fig. 83). By comparing the widths of the leaves with the lengths of the heads of the pipe-fishes in the photograph an estimate of the actual widths can be made when the dimensions of the heads of the pipe-fishes are known. This can be closely determined from museum specimens of the same species. Simple calculations based on the smallest probable lengths of the heads of the pipe-fishes photographed give the widths of the most clearly defined leaves as being over 8 mm.; this can be regarded as a conservative estimate. These leaves were thus considerably wider than any seen recently.

The conclusion that the leaves of *Zostera* were generally wider, as well as longer, is in agreement with earlier discussion on this subject (Blackburn, 1934; Cottam, 1935; Butcher, 1934, 1935) before *Z. Hornemanniana* Tutin (1936) had been recognized. It seemed then generally agreed that the *Zostera* remaining on the beds was of narrower leaf than many of the plants had formerly been. It is well known that the stature of individual plants, terrestrial and aquatic, is much influenced by the environmental conditions under which they grow and it has been suggested (Cottam, 1935, 1938; and see also Setchell, 1929)

¹ Miss E. Pearse, Paignton, has very kindly sent me a dried specimen of *Z. marina* collected in Cawsand Bay in August 1900. It has a length, exclusive of rhizome, of 3 ft. 4 in. (about 1 m). and a leaf width of about 5 mm.

that the different forms of *Z. marina* are but an expression of a varying environment. But apart from the washing away of the sand of the old banks it seems improbable that the physical and chemical conditions of the River Yealm and Plymouth Sound, to mention only localities near this laboratory, have so changed in character that the plant can no longer form broad and lengthy leaves. The hydrographic changes known to have taken place in the western English Channel might have been suspected had the phenomenon been purely local, but it was not. Everywhere, or almost everywhere, it was the broad long-leaf form which suffered most severely, leaving narrow short-leaved forms of which one subsequently proved to be a hitherto unrecognized species, *Z. Hornemanniana*. It would be interesting to know whether the broad-leaved and formerly vigorously growing variety was a definite morphological or physiological strain, which in the event proved more susceptible to the disease than did other strains.

The *Zostera* at Salcombe is, I think, spreading slowly, very slowly. No measurements are available but my impression is that there is a little more present than in the years immediately before the war when there was very little to show to the students attending the annual classes held during the Easter Vacation. To-day rather more is to be seen; it should be carefully conserved and the temptation to dig into it resisted. If left alone it may in the years to come re-establish itself and its specialized fauna with it. Unhappily, brown patches on many of the leaves can still be found, indicating that the disease is still present. It is to be hoped that the disease will become less virulent, or that a strain of *Z. marina* vigorous in growth but with high resistance to disease will some day appear to repopulate the estuaries and other sheltered waters where this useful plant was formerly abundant. On the American coast a trend toward restoration of the plant in favourable areas has been reported by Cottam (1945).

ACKNOWLEDGEMENTS

Thanks are due to a number of people who have helped by providing information, or in other ways. I am especially indebted to Mr Harry Cook of Salcombe, Mr and Mrs R. C. Tyler of East Portlemouth, and the Salcombe ferry men, Mr V. H. Ford and Mr W. Jarvis, together with a number of local people whose names I do not know. Miss C. I. Dickinson provided me with data concerning specimens of *Zostera* in the Herbarium at the Royal Botanic Gardens, Kew, and Mr R. Ross did the same for the British Museum (Natural History) collection. The assistant curators of the Plymouth City Museum and the Royal Albert Museum Exeter and the curator of the Torquay Natural History Society's museum and various private individuals have given me access to herbaria in their care. Mr T. G. Tutin kindly examined some specimens for me and confirmed an identification. To my wife I am indebted for help with botanical identifications and for the photograph reproduced in

Pl. I, fig. 1. Special acknowledgement is due to the Hydrographer to the Navy and his Department for tidal corrections for several dates. The Director, Mr F. S. Russell, has taken a kindly interest in this work throughout for which I am very grateful.

SUMMARY

A comparison of photographs taken on the eastern shore of Salcombe harbour before and after the disappearance of much of the *Zostera marina* L. shows that where previously there existed extensive sand banks, stabilized by the growth of this plant, there has been a lowering of ground level of 2 ft. or more, due to the washing away of the sand where the *Zostera* has died. Much of the ground is more stony than before and has become largely covered with seaweed attached to the stones. The buried fauna is not as rich as it was and some species previously common are rare or have disappeared altogether. A few small patches of *Zostera* still survive, but the plants are shorter with narrower leaves than before.

On the west side of the harbour there also seems to have been a similar drop in shore level at about low-water mark spring tides following the disappearance of much of the *Zostera*, and the buried fauna is also poorer than previously, but for this side no photographs and fewer data are available.

On the east side the sand washed away from the old *Zostera* banks has apparently been carried on to the higher levels to add to sand which has been steadily accumulating there for many years, especially near high-tide mark.

Plants of *Z. marina* now growing at Salcombe reach a height of about 3 ft. (about 90 cm.) in summer and have a maximum leaf width of about $\frac{1}{4}$ in. (5-7 mm.), whereas previously the plants were longer, possibly reaching 5 or 6 ft. (150-180 cm.) and had wider leaves. Plants from the estuary of the River Yealm near Plymouth certainly reached a length of 5 ft. or more, prior to 1931, and a calculation from an old photograph indicates that their leaves attained a width of at least 8 mm.

Old photographs of *Zostera* growing on soft mud near Ditch End Cove, above Salcombe harbour, show short very narrow-leaved plants which may have been *Z. Hornemanniana* Tutin.

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ADDENDA

I

Since this paper went to press the following information has been received from Major Arthur A. Dorrien Smith, Tresco Abbey, Isles of Scilly, and this seems a suitable place to record it. He has kindly given permission for this to be done.

In the Isles of Scilly *Zostera marina* was formerly abundant, covering hundreds of acres of tidal flats between the Islands, but now in 1949 scarcely any remains. The eel-grass died away about the same time as at Salcombe and elsewhere round the British coast. After its death the mud in which it grew, and which was bound by its roots and rhizomes, was loosened and washed away leaving behind nothing but sand. The drift of the tide has carried the mud into the eastern approach to the Islands, known as Crow Sound, and it has come to rest in that area. This was once an excellent trawling ground for flat fish, but it is now ruined by the mud.

2

My wife finds additional evidence of former extensive removal of sand from Salcombe in 'Kingsbridge and Salcombe, with the intermediate Estuary, historically and topographically depicted' (Kingsbridge, 1819). The anonymous author (Abraham Hawkins) says (p. 82) that 'from the bar sand

is dredged up and carried in barges to various parts of the shores of the estuary for manure. Such was the practice in husbandry formerly, that many persons recollect to have numbered thirtytwo (*sic*) of these barges on the bar at once in the years 1775-6 & 7. At present however they rarely exceed three or four.' Futhermore (p. 101), from the South Sand 'large quantities of sea-sand...are...taken at will by the occupiers of farms throughout the parish of Malborough, and carried for manure. The right is founded upon an unvarying custom time immemorial, undenied and uninterrupted, and consequently cannot now be shaken.'

EXPLANATION OF PLATES

PLATE I

Fig. 1. Decaying *Zostera* banks at about low water on 18 July 1935. Predicted level at Devonport 0.0 ft., Admiralty chart datum; observed level at Devonport 1.0 ft. higher. The approximate position from which the photograph was taken is indicated by the letter A in Text-fig. 1. The white cross occupies the same relative position as that seen on Fig. 2 below. Photograph by M. A. Wilson.

Fig. 2. View from the same position as that from which Fig. 1 above was taken, photographed at dead low water on 26 March 1948. Predicted level at Devonport 1.9 ft. below Admiralty chart datum; observed level at Newlyn 2.5 ft. higher than prediction for that port. The white cross marks the position from which the photograph reproduced in Pl. II, fig. 2 was taken.

PLATE II

Fig. 1. Collecting on a *Zostera* bank at about low water on 16 March 1926. Predicted level at Devonport 1.7 ft. below Admiralty chart datum; observed level at Devonport 1.0 ft. higher. View from position B in Text-fig. 1. The white cross marks the approximate position from which was obtained the photograph reproduced as Fig. 2 below and it therefore indicates a position on the shore identical, or almost identical, with that marked by the white crosses on Pl. I, figs. 1, 2.

Fig. 2. Collecting on the same shore at about dead low water on 26 March 1948. Predicted level at Devonport 1.9 ft. below Admiralty chart datum; observed level at Newlyn 2.5 ft. higher than prediction for that port. The position from which the photograph was taken is indicated by the white cross on Pl. I, fig. 2 and by the letter C in Text-fig. 1. It is estimated that this position would be close to the white cross on Fig. 1 above. The white cross on this photograph marks the approximate position from which the photograph reproduced in Pl. IV was obtained.

PLATE III

Fig. 1. The Ferry House and north-west corner of Small's Cove viewed from the south-west corner (position E in Text-fig. 1) on 16 March 1926.

Fig. 2. The same view as Fig. 1 on 21 May 1947, 1½ hr. before low water.

PLATE IV

View of stony and algal covered area and of residual *Zostera* beds between Small's Cove and Mill Bay, 15-20 min. after dead low water on 21 May 1947. Predicted level of low water at Devonport was 0.7 ft. below Admiralty chart datum; observed level at Newlyn 2.0 ft. higher than prediction for that port but the tide had already risen about 3 in. The area enclosed by the white dots comprised the only *Z. marina* beds exposed anywhere between the ferry and the rocks at Biddlehead. The position from which this photograph was taken is indicated by a white cross in Pl. II, fig. 2, and by the letter D in Text-fig. 1

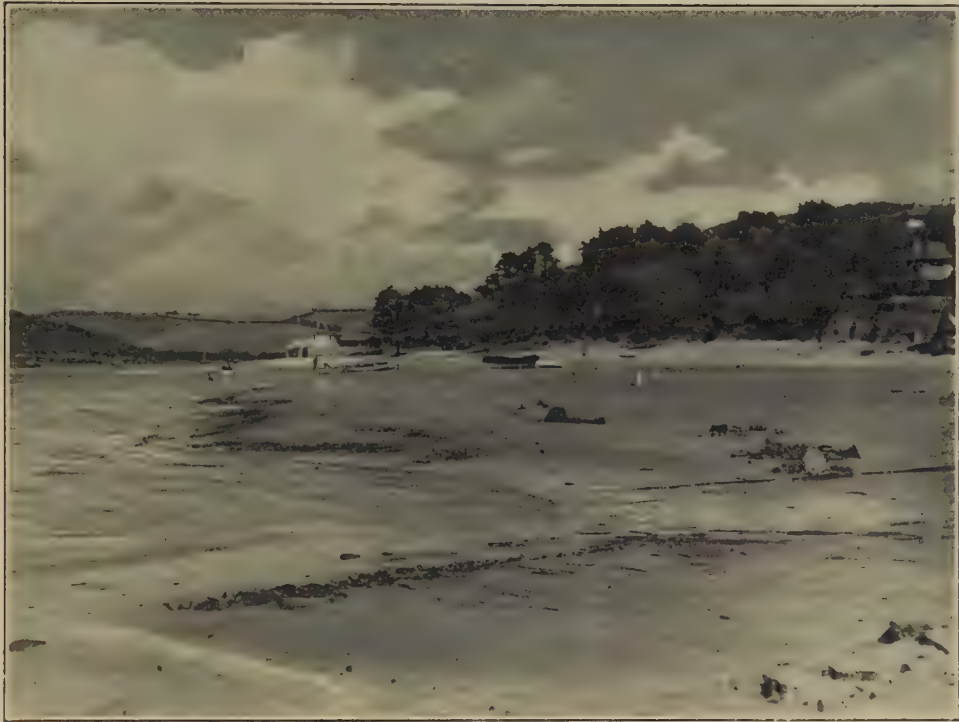


Fig. 1.



Fig. 2.



Fig. 1.



Fig. 2.



Fig. 1.



Fig. 2.



ON THE LARVAL DEVELOPMENT OF *ELMINIUS MODESTUS* DARWIN

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(Text-figs. 1-6)

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INTRODUCTION AND METHODS

Since its introduction to this country (see Bishop, 1947; Crisp & Chipperfield, 1948) the barnacle *Elminius modestus* Darwin has become numerous on Essex oyster beds. Owing to its remarkably long season of settlement and great fecundity it competes with young oyster spat for space and food more keenly than any other sessile form (Knight-Jones, 1948). It is also a dominant fouling organism of coastal craft in Essex. Workers investigating ships' fouling and oyster problems may therefore need to identify its larval stages in the plankton. These stages have not hitherto been described.

Routine plankton sampling to record the abundance and growth of oyster larvae has been carried out in the Rivers Crouch and Roach during the summers of 1947 and 1948. The standard sample used was obtained by filtering 100 l. of water, drawn from a depth of 2 m. by a 1½ in. centrifugal pump. In 1948 cirripede nauplii were abundant in these samples throughout June and July. There were often several hundred per 100 l. Bassindale (1936) recorded that nauplii which were abundant in the Plymouth plankton during the late summer were *Chthamalus stellatus* and *Balanus perforatus*. In the Burnham-on-Crouch district, however, these two species appear to be absent. We have observed only four species of barnacles, *B. balanoides*, *B. crenatus*, *B. improvisus* and *Elminius modestus*. In 1948 the main settlement of both *Balanus balanoides* and *B. crenatus* occurred in April and neither species was observed to settle after 5 June. Settlement of *Elminius modestus* and *Balanus improvisus* occurred with varying intensity from May to September, and the great majority of barnacles settling during this period were *Elminius*. Evidently the majority of the larvae which were so numerous in the plankton during the summer were *Elminius*, so the

routine 100 l. samples provided ample material for the present study. It was necessary only to distinguish larvae of *Elminius* from those of *Balanus improvisus*.

This did not prove difficult (see pp. 424-6) and of over 300 nauplii obtained from June samples and examined, no more than eighteen proved to be *B. improvisus*. All these nauplii, together with some young larvae obtained in the laboratory from adult *Elminius*, were measured by means of an eyepiece micrometer. The number of naupliar stages in the development was deduced from their size distribution. The limb setation was then studied by the method advocated by Bassindale (1936). For this purpose several nauplii of each stage were dismembered under the binocular microscope by means of fine glass needles. All drawings were made with the aid of a camera lucida.

THE NUMBER OF NAUPLIAR STAGES

Stage I nauplii were obtained by opening adult *Elminius* during June and by keeping others in aquaria. Nauplii of this stage were liberated by adults which had been living undisturbed for several days in a tank, the water of which was continually stirred. It is probable, therefore, that larvae are liberated at this stage under natural conditions. The first moult invariably occurred within 24 hr., however, and doubtless it is for this reason that very few Stage I nauplii were observed in the plankton. All batches kept in aquaria completed the first moult successfully, and Stage II nauplii were thus obtained. These and subsequent stages were also obtained from the plankton.

At the beginning of the work all cirripede nauplii which were seen in a selected plankton sample were measured. The measurements made included total length, greatest breadth and, in larvae in which the carapace fold had appeared, the length of the carapace. All measurements were taken to 0.01 of a millimetre. As work progressed it became possible to identify the larvae of *Balanus improvisus* and to judge which of those already measured belonged to this species. The data relating to these are not included here.

Presumably because of a high death-rate there were always far more younger larvae than older larvae in the samples. After measuring about 150 *Elminius* larvae it was clear that a greater proportion of early stages had been obtained and from then on only medium- and larger-sized nauplii were measured, except that occasional small specimens were measured to check that there was no appreciable difference in size between those liberated during the earlier and later parts of the season.

On examining the data it was decided that greatest breadth was the most useful measurement for identifying the various naupliar stages, since total length was affected by the degree of flexure of the abdomen, which varied considerably in different individuals, whilst carapace length could not be determined in early stages. The numbers of larvae which fell into each milli-

metre size group are given in Table I. These figures are shown graphically in Fig. 1. As already indicated, the larvae measured did not constitute a single random sample. Larvae measuring 0.14 mm. or less were obtained only from batches liberated in aquaria. A few of those measuring 0.15–0.17 mm. were obtained in the same way. The plankton samples from which the remainder were obtained were taken on several different dates during June and July, and

TABLE I

Greatest breadth (mm.)	No. of larvae	Greatest breadth (mm.)	No. of larvae	Greatest breadth (mm.)	No. of larvae	Greatest breadth (mm.)	No. of larvae
0.11	2	0.19	23	0.27	5	0.35	9
0.12	11	0.20	10	0.28	10	0.36	13
0.13	10	0.21	0	0.29	9	0.37	3
0.14	2	0.22	5	0.30	10	0.38	3
0.15	4	0.23	9	0.31	12	0.39	2
0.16	25	0.24	27	0.32	0	0.40	2
0.17	10	0.25	7	0.33	3	0.41	1
0.18	8	0.26	2	0.34	8		

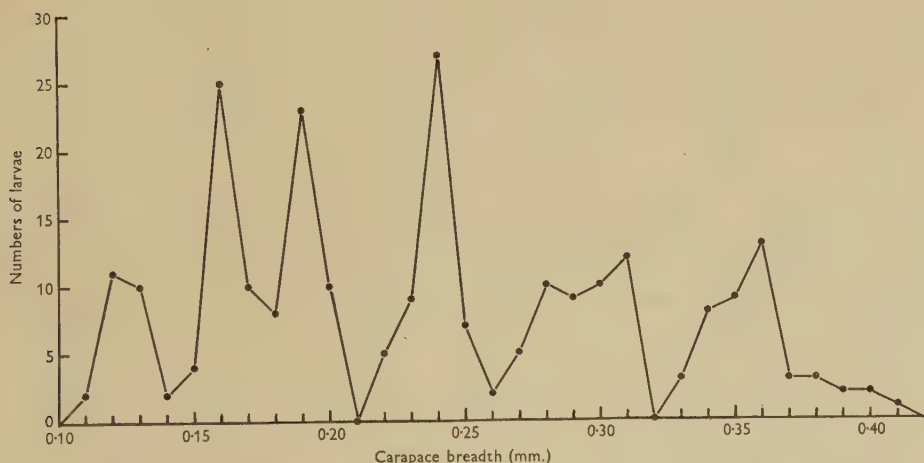


Fig. 1. The size distribution, in 0.1 mm. groups, of all *Elminius* nauplii measured (245). The larvae did not constitute a single random sample, but such general selection as was exercised in obtaining them cannot account for the presence on this graph of six distinct peaks. These indicate that there are six naupliar stages in the development. This was corroborated by morphological study. The naupliar stage to which each size group belonged can be seen from Table II. In respect of this measurement (carapace breadth) no overlapping in size between successive stages was observed.

often only the larger larvae seen in a sample were measured. This selection was exercised only in a general way, to ensure that all sizes of larvae were adequately represented in the sample. Such general selection cannot account for the presence on this graph of six distinct peaks. These indicate that there are six naupliar stages in the development and that the later stages are much more

variable in size than the earlier stages. The graphic evidence for six naupliar stages is corroborated by the determination of six distinct setation formulae (Table III, p. 420).

THE IDENTIFICATION OF THE NAUPLIAR STAGES

The size limits observed for each stage are given in Table II. The measurements of carapace length included the length of the carapace spines, which varied rather widely between 0.015 and 0.045 mm., but was usually 0.02 or 0.03 mm. The measurements of total length showed much overlapping between successive stages, since the degree of flexure varied and was sometimes extreme, but other measurements afforded a fairly reliable means of identifying the stages. The limb setation of each stage is also characteristic, but this cannot be

TABLE II. MEASUREMENTS OF LARVAL STAGES OF *ELMINIUS MODESTUS* IN MM.

Stage	Carapace		Full length
	Greatest width	Length	
I	0.11-0.14	—	0.24-0.26
II	0.15-0.17	—	0.36-0.43
III	0.18-0.20	0.21-0.25	0.35-0.43
IV	0.22-0.25	0.29-0.35	0.39-0.50
V	0.26-0.31	0.34-0.44	0.45-0.57
VI	0.33-0.41	0.42-0.55	0.48-0.71
Cyprid	—	0.54-0.56	—

studied accurately without dissection. It is better to rely for identification on the following more general characters, many of which are similar to those described for other species by Bassindale (1936) and Pyefinch (1948).

Stage I nauplii are rounded anteriorly with the fronto-lateral horns pointing obliquely backwards. The caudal spine and abdominal process (to use the terms adopted by Pyefinch) are short (Fig. 2). The frontal filaments are not yet developed. The limb setae are unfeathered (Fig. 5). In subsequent stages the fronto-lateral horns point in a lateral or antero-lateral direction, the caudal spine and abdominal process are well developed, the frontal filaments are obvious and many of the limb setae are feathered.

Stage II nauplii are characteristically slender with a particularly long caudal spine and a shorter, narrow abdominal process. The prongs of the forked abdominal process are proportionately longer than in the other stages. There is no sign of a posterior edge to the carapace.

Stage III nauplii are of the same total length as those of Stage II but are of stouter build. The posterior edge of the carapace is well defined and bears a carapace spine on each side of the mid-dorsal line. There is no projecting carapace fold, however, so the carapace spines are closely applied to the body and often difficult to distinguish at this stage. The abdominal process is slightly swollen at the base and is about the same length as the caudal spine. In both

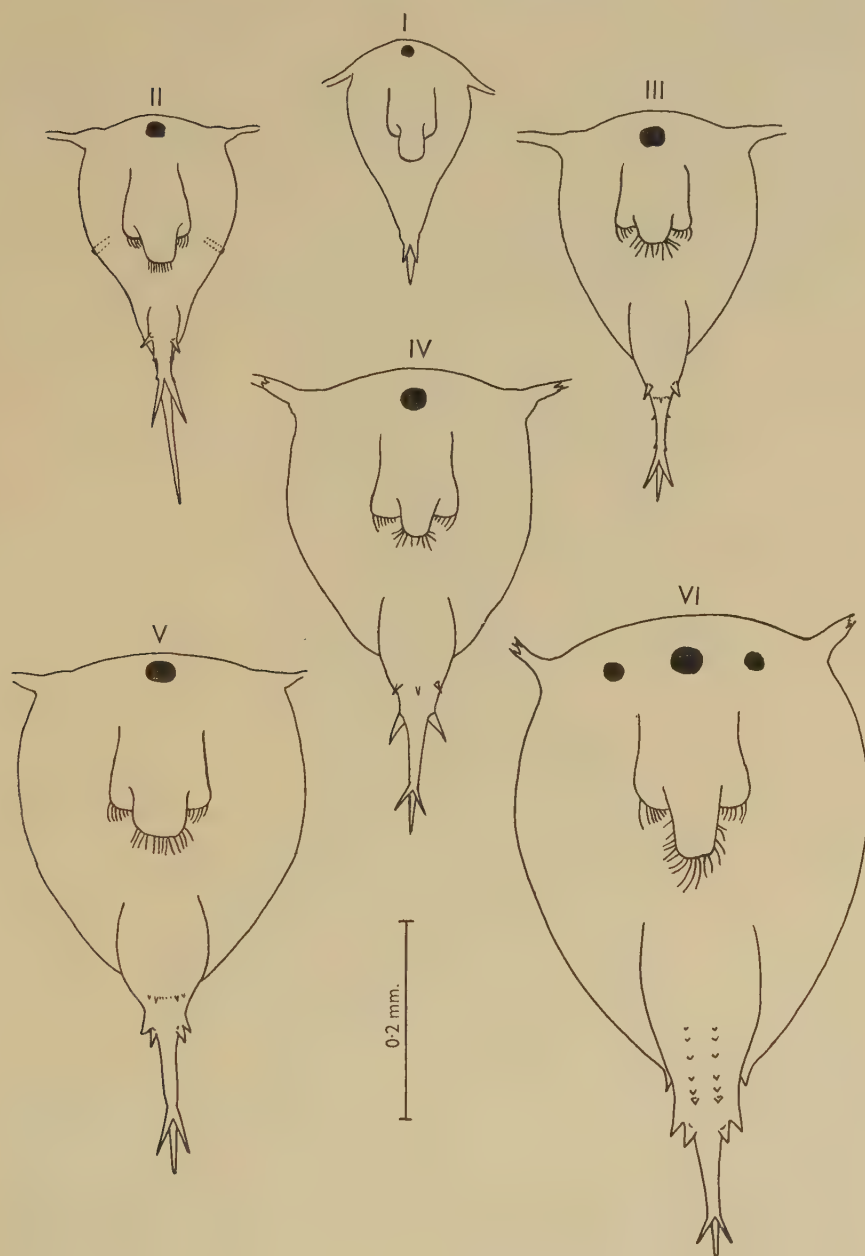


Fig. 2. *Elminius modestus*. Outline drawings of the six naupliar stages, showing the labrum, all to same scale.

Stages II and III there is a single pair of large spines on the latero-ventral surface of the abdomen.

Stages IV, V and VI possess in common a rounded shape and a carapace of which the posterior border juts out prominently and bears a pair of carapace spines. There are two pairs of prominent spines on the latero-ventral surface of the abdomen. In Stage IV these two pairs are comparatively widely separated and the anterior pair is smaller than the posterior pair. In Stages V and VI they are close together and similar in size. During these three stages the base of the abdominal process becomes increasingly swollen, and in Stage V the internal rudiments of the abdominal appendages can be distinguished.

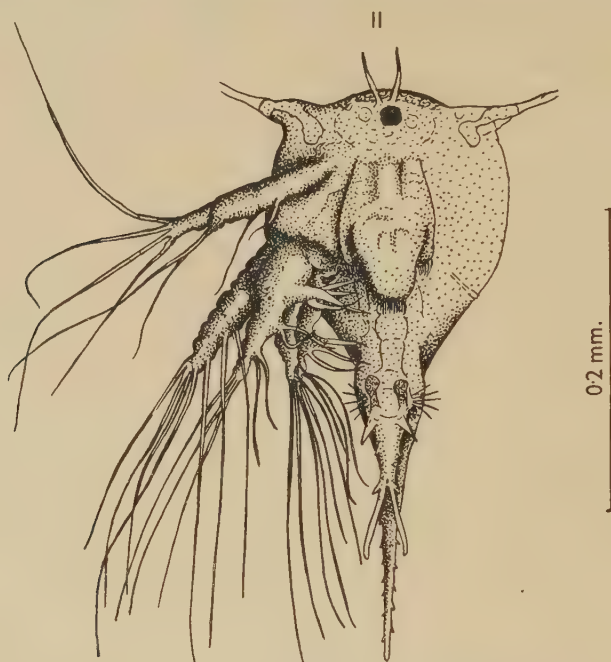


Fig. 3. *Elninius modestus*. Stage II nauplius, showing limbs of right side only, ventral aspect. Nauplius is transparent.

In Stage VI metanauplii the six pairs of abdominal appendages are prominent. Anterior to these the setae of the maxillulae can be distinguished. The ventral surface of the abdomen bears six pairs of small spines, which appear to be segmentally arranged. Older metanauplii are readily recognized by their three black eye spots, but in many larvae of this stage no paired eyes can be distinguished and in others the paired eyes are not fully pigmented and are red in colour.

Fig. 2 gives outline drawings of typical specimens of each stage all drawn to the same scale. Fig. 3 shows a Stage II nauplius in greater detail. Fig. 4 is a side view of a Stage VI nauplius and a cyprid.

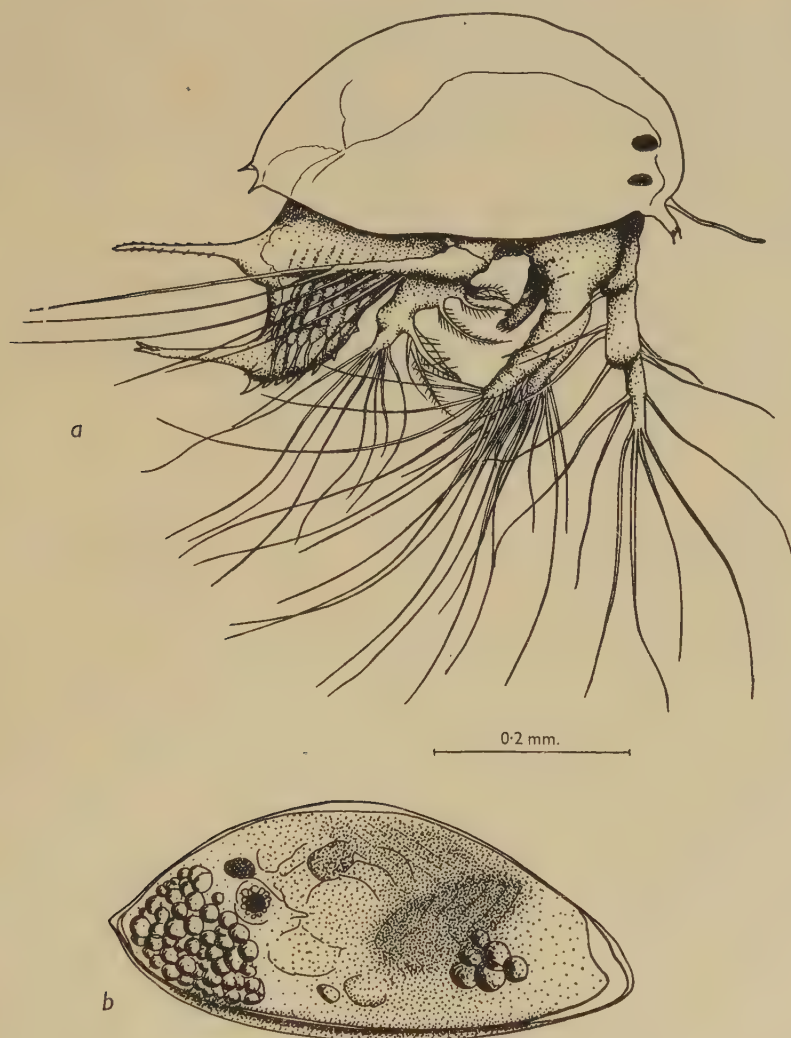


Fig. 4. *Elminius modestus*. a, Stage VI nauplius, right side; b, cyprid larva, left side.

LIMB SETATION

Bassindale (1936) wrote as follows:

In order to facilitate a comparison of barnacle nauplii a setation formula has been elaborated. The setae on the appendages of cirripede nauplii occur in groups along the dorsal and ventral sides of the appendages. Each group has been represented by a figure giving the actual number of setae present. The formula is obtained by arranging these numbers in order, reading from the base of each appendage along the dorsal edge of the exopodite, down its ventral edge, and then up the dorsal and down the ventral edges

of the endopodite. [Compare Table III with Figs. 5 and 6.] The setae at the tip of each ramus are indicated by black figures representing the group; the formulae for the two rami are separated by a dash and those for different appendages by a semicolon. The appendages are taken in order from the anterior end. The gnathobase occurring on the antenna and mandible is represented by G. On the exopodites of the antenna and mandible each of the distal segments bears one strong swimming-seta. In order to contract the formula these are expressed as one group, the terminal seta or setae alone being separated. Instead, therefore, of reading 0.1.1.1.1.1.1.1. the formula reads 0.1.6.

Variations in the number of setae in some groups are found. This is usually due to the precocious development of a seta normally appearing at the next stage or to the delayed development of a seta. Differences of more than one seta in any one group have not been observed.

TABLE III. SETATION FORMULAE FOR THE LARVAL STAGES OF *ELMINIUS MODESTUS*

Stage	Antennule	Antenna	Mandible
I	0.4.2.1.1;	0.1.4-0.3.2.2.2.G;	0.1.3-0.3.2.2.2.G
II	0.4.2.1.1;	0.1.6-0.3.2.2.3.G;	0.1.3-0.3.2.3.2.G
III	1.4.2.1.1;	0.1.6-0.3.2.2.4.G;	0.1.4-0.3.3.3.3.G
IV	1.1.4.2.1.1;	0.2.7-0.5.3.2.4.G;	0.1.4-0.4.3.3.3.G
V	2.1.4.2.1.1.1;	0.3.8-0.5.3.2.4.G;	0.1.5-0.4.4.4.3.G
VI	2.1.4.2.1.2.1;	0.4.8-0.5.3.2.4.G;	0.1.5-0.4.4.4.3.G

Bassindale gave setation formulae for all stages of *Balanus balanoides*, *Verruca stroemia* and *Chthamalus stellatus*, and also gave some data for *Balanus crenatus* and *B. perforatus*. It therefore seemed desirable to work out the setation formulae for the stages of *Elminius*, following the same method. From five to ten specimens of each stage were dismembered and examined. No discrepancies were observed, so the setation appears to be remarkably constant for each stage, as in other species so far described. The formulae are given in Table III.

The brevity of the setation formula makes it a useful instrument for the comparative study of cirripede nauplii (see p. 424 for a brief discussion of its limitations), but it may be somewhat misleading to describe each seta, whatever its size, as a similar unit, for the setae differ greatly from one another in size and form. Some are stumpy, some are feathery bearing numerous setules, whilst some are bare and extremely fine, and some are small. In order to ascertain the setation formulae with certainty it proved necessary to draw each limb in detail. In Figs. 5 and 6 these drawings are reproduced, all to the same scale.

COMPARISON WITH ALLIED FORMS

Bassindale (1936) described the naupliar stages of *Balanus balanoides*, *Chthamalus stellatus* and *Verruca stroemia*, compared them with those of *Balanus perforatus* as described by Groom (1894) and gave data for several other species. Pyefinch (1948) compared larvae of *B. balanoides*, *B. crenatus* and *Verruca stroemia*, with special reference to characters which can be recognized at a glance under

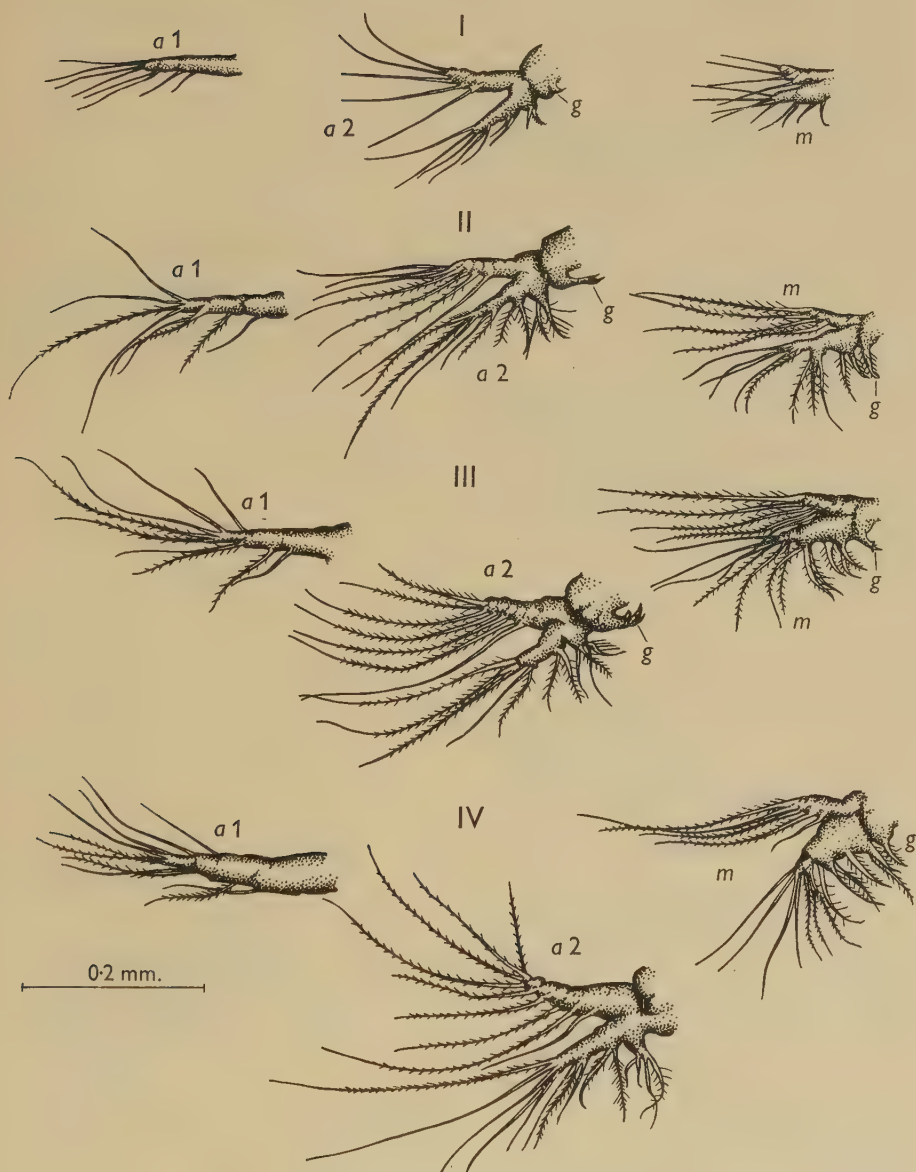


Fig. 5. *Elminius modestus*. The limbs of naupliar Stages I-IV; antenna 1 (a 1) on the left, antenna 2 (a 2) in the centre; mandible (m) on the right; g, gnathobase.



Fig. 6. *Elminius modestus*. The limbs of naupliar Stages V and VI; a 1, antenna 1; a 2, antenna 2; m, mandible; g, gnathobase.

a low-power binocular microscope. Herz (1933) had described the development of *Balanus crenatus*, but the work of Bassindale and Pyefinch suggests strongly that he was wrong in ascribing eight naupliar stages to these species. Pyefinch found that *B. crenatus* in the Clyde passed through only six naupliar stages, like every other species of barnacle so far described. We have not examined the larvae of these species, but it may be useful to draw attention to the points in which *Elminius* larvae differ from the published descriptions of them. The only species which was observed in our plankton samples from June onwards, besides *Elminius*, was *Balanus improvisus*. No adequate description of the larvae of this species is yet available in this country. The figures of Stages I and II given by Buchholz (Münter & Buchholz, 1870) and reproduced by Hoek (1909) are somewhat schematic and the limb setation is inaccurately reproduced. Figures of later stages by Filatowa (1902) and Tengstrand (1931) are too small to be of value, and we were not able to consult the account of Lucks (1940), referred to by Thorson (1946) as figuring Stages IV and VI and the cyprid.

We have obtained Stage I nauplii from adult *B. improvisus*. They moulted overnight to give Stage II nauplii and we also observed this stage in the plankton of the River Crouch and the River Conway (North Wales). We examined one larger larva from the plankton which was not *Elminius modestus* and did not agree with the description of any other form. It had abdominal appendages clearly visible within the cuticle of the swollen abdomen, and it was probably the stage of *Balanus improvisus* immediately preceding the metanauplius, i.e. probably a Stage V nauplius.

The following appear to be the main points of comparison between the larvae of *Elminius modestus* and those of native barnacles.

Size

The particularly squat nauplii of *Chthamalus* are so much shorter and the bulky nauplii of *Balanus balanoides* so much larger than those of *Elminius modestus* that it is unnecessary to go further into the differences between these species in size and shape. *Balanus crenatus* larvae from the Clyde are also markedly larger than the corresponding stages of *Elminius modestus*, whilst *Balanus perforatus* and *Verruca stroemia* are slightly larger. The larvae of *Elminius modestus* and *Balanus improvisus*, however, are very similar in size.

Shape

The later stages of *Verruca* are unlikely to be confused with those of *Elminius* because *Verruca*, like *Chthamalus*, has a short rounded carapace and no carapace spines. A Stage II *Verruca* differs from that of *Elminius* in possessing a much longer abdominal process which reaches to the end of the caudal spine. A Stage III *Verruca* is considerably longer than any *Elminius* stage younger than Stage IV, and is quite unlike a Stage IV *Elminius* in having no posterior edge to its carapace.

The larvae of *Balanus improvisus*, *B. crenatus* and *B. perforatus* resemble the corresponding stages of *Elminius modestus* fairly closely in general shape. A Stage II *E. modestus* can be distinguished, however, by its long caudal spine and short abdominal process (Fig. 3). In *E. modestus* of this stage the caudal spine is longer than the abdominal process by 0.06–0.10 mm. In *Balanus improvisus* the caudal spine is longer by only 0.01–0.05 mm., and in *B. crenatus* the difference in length appears to be smaller still. Although the total length of the abdominal process in Stage II of *Elminius modestus* is comparatively small the prongs of the forked terminal portion (included in the total length) are of great relative length and comparatively great absolute length (0.05–0.06 mm.). In *Balanus improvisus* they are only 0.03–0.04 mm., and in all other British species of barnacle so far described they appear to be shorter still.

In *B. perforatus*, Stages II and III, the outline is unlike that of *Elminius* and of other native species of *Balanus* so far described, in that there is a distinct notch in the lateral margin on each side. This is shown in Groom's figures (1894) of Stages II and III, and Lochhead's figure (1936) of Stage II, all seen in ventral view. It appears to correspond to the posterior margin of the carapace.

In *Elminius modestus* the great length of the caudal spine in Stage II is foreshadowed by a slight elongation of this region in Stage I. Nauplii of the corresponding stages of *Balanus improvisus*, though similar in width to *Elminius modestus*, are shorter. Measurements of a few larvae of *Balanus improvisus* from the River Crouch and from the estuary of the River Conway, North Wales, were as follows:

	Greatest width (mm.)	Total length (mm.)
Stage I	0.13	0.20–0.21
Stage II	0.15–0.16	0.33–0.36

Limb setation

Bassindale, after giving the setation formulae for Stages I and II of *B. crenatus* and *B. perforatus*, remarked that 'a close comparison of these formulae with those for *B. balanoides* indicates the close similarity of the nauplii which are also similar in general shape and size'. This seems to imply that the similarity between the setation formulae of the early stages of these three species confirms that their taxonomic relationship is close. Such an interpretation is misleading, for the formulae which he gave for the same stages of *Chthamalus* and *Verruca* are also very similar to each other and to those given for *Balanus*.

It now appears that there is remarkable resemblance between the setation formulae of the earlier stages of all barnacles which have so far been studied. This is shown in Table IV. The formulae for *Elminius modestus* and *Balanus improvisus* were derived from specimens from the River Crouch, the remainder are taken from Bassindale (1936). It will be seen that the formula for Stage I nauplii of *Elminius modestus* is identical with that of *Balanus improvisus*, and

with that given by Bassindale for *B. crenatus*. Otherwise there are small differences at both stages between *Elminius modestus* and the various species of *Balanus*, although these barnacles are all closely related, being included in the same family (Balanidae). On the other hand, the formulae for Stage II nauplii of *Elminius modestus* (Balanidae), *Chthamalus stellatus* (Chthamalidae) and *Verruca stroemia* (Verrucidae) are identical. Evidently the small differences and resemblances between the setation formulae of the early larvae of different species are of no systematic importance within these three families.

The formulae for the later stages of *Elminius modestus* (and of barnacles generally) are more distinctive, although that of Stage III nauplii of *Elminius* is identical, and that of Stage IV nauplii almost identical, with those given for the corresponding stages of *Chthamalus stellatus* (another point of resemblance which extends across an accepted taxonomic division).

TABLE IV. THE SETATION FORMULAE FOR THE FIRST TWO NAUPLIAR STAGES OF SEVEN COMMON SPECIES OF BARNACLE

Species	Stage	Antennule	Antenna	Mandible
<i>Balanus balanoides</i>	I	0.4.2.1.1;	0.1.4-0.3.2.2.2.G;	0.1.3-0.3.2.3.2.G
	II	0.4.2.1.1;	0.1.6-0.3.2.2.2.G;	0.1.3-0.3.3.3.2.G
<i>B. perforatus</i>	I	0.4.1.1.1;	0.1.4-0.3.2.2.2.G;	0.1.3-0.2.1.2.2.G
	II	0.4.2.1.1;	0.2.5-0.3.2.2.3.G;	0.1.3-0.3.2.3.2.G
<i>B. crenatus</i>	I	0.4.2.1.1;	0.1.4-0.3.2.2.2.G;	0.1.3-0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6-0.3.2.2.2.G;	0.1.3-0.3.2.3.3.G
<i>B. improvisus</i>	I	0.4.2.1.1;	0.1.4-0.3.2.2.2.G;	0.1.3-0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6-0.3.2.2.3.G;	0.1.4-0.3.2.3.2.G
<i>Elminius modestus</i>	I	0.4.2.1.1;	0.1.4-0.3.2.2.2.G;	0.1.3-0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6-0.3.2.2.3.G;	0.1.3-0.3.2.3.2.G
<i>Chthamalus stellatus</i>	I	0.4.1.1.1;	0.1.4-0.3.2.2.2.G;	0.1.3-0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6-0.3.2.2.3.G;	0.1.3-0.3.2.3.2.G
<i>Verruca stroemia</i>	I	0.4.2.1.1;	0.1.4-0.3.2.2.3.G;	0.1.3-0.3.2.2.2.G
	II	0.4.2.1.1;	0.1.6-0.3.2.2.3.G;	0.1.3-0.3.2.3.2.G

Because of this close resemblance between species and because the study of the limb setation of barnacle nauplii is at present incomplete, Bassindale's formula can safely be used only for confirming an identification made on other grounds, and for distinguishing between the different stages of a given species.

Labrum

In *Ch. stellatus*, and in *Verruca stroemia*, the labrum is a single tongue-shaped lobe with a rounded posterior end. In *Balanus*, in all stages except the earliest, the labrum is more or less square posteriorly. The labrum figured by Bassindale for Stage II nauplii of *B. balanoides* has three lobes, but the median lobe does not extend posteriorly beyond the lateral lobes so it does not interrupt the square shape. In his figure for Stage V nauplii of this species, no median lobe is shown. Stages I and II nauplii of *B. improvisus* also have a trilobed labrum, with a median lobe which does not extend posteriorly beyond the lateral lobes.

The single large nauplius which we observed in the plankton and which was probably a Stage V of *B. improvisus* had a square labrum with no obvious median lobe. In all stages of *B. crenatus* (Herz, 1933) and in all stages, except the first, of *B. perforatus* (Groom, 1894) the labrum is trilobed, but the median lobe extends posteriorly only slightly beyond the lateral lobes.

In all naupliar stages of *Elminius modestus* the labrum is obviously trilobed with a long median lobe which extends posteriorly much farther than the lateral lobes. This character clearly marks out *E. modestus* larvae from those of all species so far described, but in using it to distinguish between *E. modestus* and *Balanus improvisus* (two species of which the nauplii are particularly liable to be confused), two pitfalls must be avoided. First, in Stages I and II of *B. improvisus*, although the median lobe of the labrum does not project posteriorly, it projects prominently in a ventral direction. It appears very prominently, therefore, in specimens of *B. improvisus* which are standing on their heads in a dish of plankton and which are being viewed posteriorly. Secondly, in many preserved specimens of *Elminius modestus*, the labrum projects from the body at an obtuse angle. The median lobe is then foreshortened in ventral view and the labrum may appear square. It follows that when using the form of the labrum to distinguish between these two species, each specimen should be viewed from the ventral direction. If the labrum is markedly trilobed, *E. modestus* is indicated. If it appears square, the specimen should be viewed under a supported cover-slip to ensure that the labrum is lying more or less flat. If it still appears square, *Balanus improvisus* is indicated.

The cyprid

The cyprid of *Elminius modestus* is colourless and of glassy transparency. Those from the River Crouch were 0.54–0.56 mm. long. This is larger than the size which Bassindale gave for the cyprid of *Chthamalus stellatus*. It resembles in size that of *Verruca stroemia*, but differs in shape (see Fig. 4*b*) from the figure given by Pyefinch for this species, which showed a straight postero-dorsal margin and a pointed posterior end. It is much smaller than that of *Balanus balanoides* and distinctly smaller than that of *B. crenatus* in British waters and of *B. perforatus*. It resembles in size that of *B. improvisus*. Tengstrand (1931) gave the length of this cyprid as 0.6 mm., in Swedish waters. A cyprid from the River Crouch, which was probably this species, was 0.53 mm. long. This specimen was quite unlike a cyprid of *Elminius modestus* in being opaque and in having a blunter posterior end.

The later nauplii of *Elminius* thus resemble those of *Balanus* and differ from those of *Chthamalus* and *Verruca* in possessing a trilobed labrum and a fairly long carapace tapering posteriorly and bearing on its posterior margin a pair of carapace spines. They do not differ from those of *Balanus* in any important

respect. Darwin (1854) suggested a close affinity between *Elminius*, *Tetraclita* and *Balanus*. He wrote that *Elminius* 'can be distinguished from *Tetraclita* only by the four compartments not being porose and by the basis being always membranous', and that *Tetraclita* 'is closely allied to *Balanus*; I can point out no difference in the animal's body, nor any constant difference in the opercular valves'.

The development of *Elminius* tends to confirm that this genus is closely related to *Balanus*.

SUMMARY

Nauplii of the first two stages were obtained from adult *Elminius modestus* and larvae of all stages, except the smallest, were obtained from the plankton over Essex oyster beds.

Over 200 nauplii of all sizes were measured. Their size distribution, plotted graphically, showed six peaks corresponding to six naupliar stages. The later stages were much more variable in size than the earlier stages.

The size limits and characteristics of each naupliar stage are given. Briefly, Stage I has the fronto-lateral horns pointing backwards. Stage II has the caudal spine much longer than the abdominal process. Stage III has the abdominal process about as long as the caudal spine, but has no carapace fold posteriorly. Stage IV has a carapace fold but no sign of the abdominal appendages. Stage V has the rudiments of these appendages showing indistinctly within the abdomen. In Stage VI the abdominal appendages are prominent.

The limb setation of each stage is figured and described according to Bassindale's formula. The taxonomic value of this formula is limited, since there is a remarkable resemblance between the formulae for the early nauplii of all species so far studied.

The larvae are compared with those of other barnacles of which the development has been described. In general, they resemble those of *Balanus*, but they are much smaller than those of *B. balanoides* and distinctly smaller than those of the corresponding stages of *B. crenatus* in the Clyde and *B. perforatus* in the English Channel. They are most likely to be confused with those of *B. improvisus*, which they resemble in size. The shape of the labrum is the most distinctive feature of *E. modestus* nauplii. It is trilobed, with the median lobe extending posteriorly much farther than the lateral lobes.

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A STATISTICAL STUDY OF THE VARIATION IN VERTICAL PLANKTON HAULS, WITH SPECIAL REFERENCE TO THE LOSS OF THE CATCH WITH DIVIDED HAULS

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(Plates I, II and Text-figs. 1-6)

INTRODUCTION

Although in some branches of marine biology statistical methods have been extensively employed in considering the sampling variations so frequently encountered, little attention has yet been paid to the study of such variations arising in plankton work. Gardiner (1931), and particularly Winsor & Walford (1936), Winsor & Clarke (1940) and Silliman (1946), have given some consideration to the problem, and an account of a freshwater plankton investigation in which the techniques were carefully chosen and the results critically examined by statistical methods has been given by Baldi, Cavalli and Pirocchi (1945). Early work by Hensen (1887, 1900-12), Lohmann (1903), and Herdman (1921) indicated the order of variation to be expected in vertical hauls.

The material on which the following analysis is based was obtained by Marshall, Nicholls & Orr and some of the results of the work have already been given (1934). A further account of the material has recently been given by Marshall (1949), where all the raw data dealt with here may be found. The discrepancy observed between the total catch in divided and undivided hauls was a puzzling feature of these results, and subsequent to discussions with Dr Marshall on the origin of this discrepancy she placed at my disposal for analysis the whole of the data. Thanks are due to Dr Marshall not only for providing the data but also for giving further details of the technique and circumstances of the collections. It is also a pleasure to acknowledge the assistance of Dr R. A. Robb, who read the manuscript at several stages of its preparation and who, by his critical comments and advice, has enhanced its value.

The material was all collected by means of a net hauled vertically. Some details of the work have been given in the references already cited, but since the analysis will be of use to other workers only if the conditions under which the hauls were made are precisely defined, the salient features of the technique must be summarized.

(i) The hauls were made with a modified international net fitted with a Nansen (1915) closing mechanism. The net differed from the standard

pattern in the absence of a coarse net band above the canvas band carrying the throttling device.

(ii) Hauling was by hand winch.

(iii) The speed of hauling was controlled by timing the rate of haul (depth being followed by means of the metre wheel) with a stop-watch, instructions being shouted to the person working the winch. An attempt to maintain a hauling speed of 0.5 m./sec. was made.

(iv) The bucket used on the net was a simple metal cylinder tied on with string.

(v) After completion of the haul the catch was washed into the bottom of the net by moving the latter up and down in the water, without, of course, allowing the mouth of the net to go under the surface of the water.

(vi) The bucket was then carefully removed and the contents emptied into a breffit containing formalin. The bucket was then rinsed out several times with sea water from a pail and the washings added to the catch; the canvas portion at the base of the net was then turned back exposing the lower portion of the net and, with this held over the breffit, all obvious organisms were carefully removed and the whole washed down several times.

(vii) In taking the divided hauls an attempt was made to release the messenger so that the net would close at the selected depth without any interruption of the hauling.

(viii) The weather conditions under which the catches were made varied throughout the season; the stations worked were inside a comparatively sheltered sea loch and at no time during this particular series were the conditions very bad.

(ix) The depth of the haul was of the order of 60 m., and its duration approximately 2 min. If 5 min. for removing the catch is allowed, this gives a period of about 10 min. in which to obtain duplicate hauls.

(x) Counts of the developmental stages of the following copepods were made and have been used in the analysis: *Pseudocalanus minutus* (Krøyer), *Microcalanus pygmaeus* G. O. Sars, *Centropages hamatus* (Lilljeborg), *Temora longicornis* (Müller), *Acartia clausi* Giesbrecht, *Oithona similis* (Claus).

It should be stated that this work was not originally planned for statistical treatment, and a selection of the data will be presented to illustrate the problems involved and their possible solution.

THE UNDIVIDED HAULS

Three pairs of duplicate undivided hauls will now be considered and the data are plotted as the log of the catches for the separate stages of each pair of hauls in Fig. 1. In each of the catches eight stages of the six species were counted so that, neglecting those pairs in which the total number caught ($n_1 + n_2$) was less than 5, there are 134 pairs of observations, each stage of every species being

considered independently. The results obtained with these undivided hauls will first be compared with the data analysed by Winsor & Walford (1936) using counts of a series of catches of fish eggs (the E-S series) and the data obtained in the course of investigations of catching powers of different types of nets by Künne (1929, 1933). The problem, as pointed out by these authors,

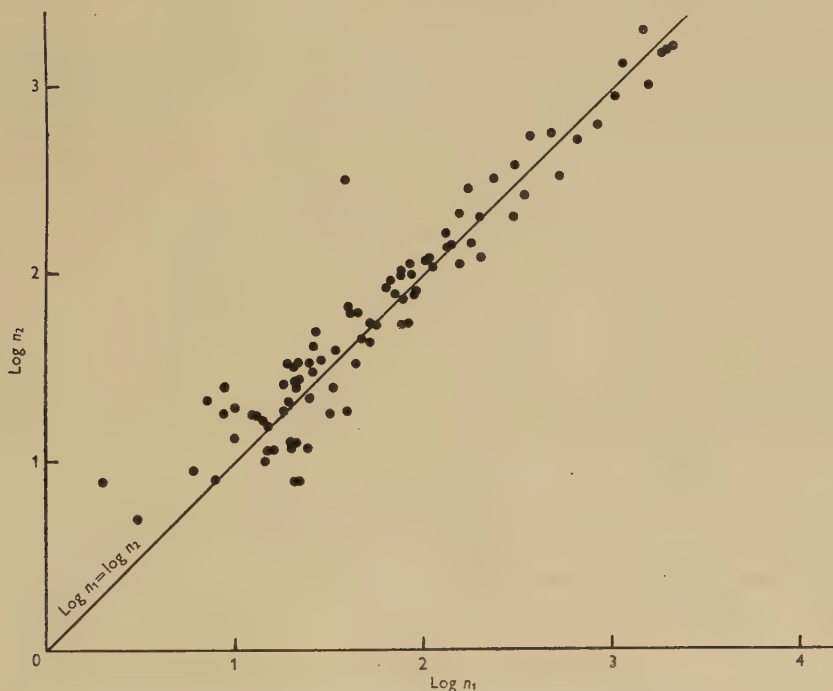


Fig. 1. The relationship between pairs of catches of all stages of six copepods for three sets of duplicate vertical hauls, plotted as logarithms of the catches.

is similar to that of the estimation of bacterial numbers, the basic distribution of which, when the experimental technique is adequately controlled, has been shown by Fisher, Thornton & MacKenzie (1922) to be Poisson. The value has therefore been calculated, for each pair of observations, of

$$\chi^2 = \frac{(n_1 - n_2)^2}{(n_1 + n_2)}, \quad (1)$$

where n_1 and n_2 are the numbers of each stage in a pair of duplicate hauls and when $(n_1 + n_2) > 10$. When $5 < (n_1 + n_2) < 10$ an adjusted value of χ^2 has been used,

$$\chi^2 = \frac{(n_1 - n_2)^2 - 2(n_1 - n_2) + 1}{(n_1 + n_2)}. \quad (2)$$

Pairs in which $(n_1 + n_2) < 5$ have been neglected.

If the basic distribution were truly Poisson this χ^2 should, in a number of random samples, have a mean value of 1 and should be distributed in a known manner. For comparison with the data of Winsor & Walford similar classes of χ^2 have been selected and the distribution of this quantity is shown in Table I.

TABLE I. DISTRIBUTION OF VALUES OF χ^2 (134 PAIRS).

$$\chi^2 = \frac{(n_1 - n_2)^2}{(n_1 + n_2)}, \quad \text{when } (n_1 + n_2) > 10;$$

$$\chi^2 = \frac{(n_1 - n_2)^2 - 2(n_1 - n_2) + 1}{(n_1 + n_2)}, \quad \text{when } 5 < (n_1 + n_2) < 10;$$

$$(n_1 + n_2) < 5 \text{ neglected.}$$

χ^2	Proportion of values expected (Poisson)	Number of values observed	Proportion of values observed
0-0.016	0.1	6	0.045
-0.064	0.1	6	0.045
-0.148	0.1	7	0.052
-0.275	0.1	3	0.022
-0.455	0.1	9	0.067
-0.708	0.1	8	0.059
-1.074	0.1	9	0.067
-1.642	0.1	12	0.089
-2.706	0.1	16	0.119
-6.635	0.09	30	0.223
> 6.635	0.01	28	0.209

This distribution is far from theoretical for Poisson, and is similar to that obtained by Winsor & Walford. The fact that there is an excess of large values of χ^2 shows that there is an excess of samples showing relatively large differences between hauls.

TABLE II. VALUES OF TOTAL AND MEAN χ^2 FOR VARYING SAMPLE SIZE

$(n_1 + n_2)$	Number of samples	$S\chi^2$	$\bar{\chi}^2$
5-10	18	44.57	2.48
-20	8	15.68	1.96
-40	24	68.69	2.86
-60	18	43.73	2.43
-80	10	21.26	2.13
-170	16	35.53	2.22
-400	19	69.08	3.64
-1000	9	161.51	17.83
> 1000	12	1726.15	143.85

In Table II the mean values of χ^2 have been tabulated by size groups and the results are again similar to those of Winsor & Walford. Thus, the large hauls furnish a larger proportion than expected of the high values of χ^2 as shown by the increase in the mean χ^2 with increasing size of sample. It seems clear that other factors than the sampling variations of a random population are affecting the hauls.

Assuming that the most important factor contributing to these variations is the volume of water filtered (or at least affecting the sample by its effect on the volume filtered) Winsor & Walford derive the following expression for χ^2 :

$$\chi^2 = 1 + n \frac{\sigma_v^2}{\bar{v}^2} = 1 + K^2 \bar{n}, \quad (3)$$

where $\bar{n} = \frac{1}{2}(n_1 + n_2)$, σ_v = standard deviation of volume, $\bar{v}$ = mean volume filtered.

There is little change in the value of χ^2 up to $(n_1 + n_2) = 170$, with the present data, and beyond this point the size of these groups has to be greatly increased to obtain a reasonable number of samples. Grouping together gives Table III.

TABLE III

$(n_1 + n_2)$	Number of samples	$S\chi^2$	$\bar{\chi}^2$
0-170	94	229.44	2.44
170-400	19	69.08	3.64
400-1000	9	161.51	17.83
>1000	12	1726.15	143.85

These values are plotted in Fig. 2, and although the number of points is inadequate they can be considered as lying on a straight line passing through the point $\bar{\chi}^2 = 1$, when $\bar{n} = 0$. The equation of this line gives a value for the constant K^2 of 0.05. The value suggested by Winsor & Walford for K^2 is 0.04-0.06 and they emphasize the fact that K is not a universal constant. The agreement of the value calculated from the present data with their value is very satisfactory.

Since the coefficient of variation of a single observation is

$$\frac{\sigma}{n} = 100 \sqrt{\left(\frac{1}{n} + K^2\right)},$$

then putting $K^2 = 0.05$, and for a total catch of 100 ($n = 100$),

$$\frac{\sigma}{n} = 25\%.$$

The above agreement appears to suggest that the basic assumption, namely a random distribution of the population, holds for the present series, and that the variations between the hauls are largely due to differences in the volumes of water filtered. It follows that since different stages of a number of species were counted, all are randomly distributed, that is, there is no association between any of the animals or their various stages. This does not mean that changes in density do not take place in a vertical direction but only that at any point in the vertical section there is a random distribution of the species and their separate stages.

An alternative method of analysing the results of such replicate hauls is possible and has been employed by Winsor & Clarke (1940). Both new data

and that previously considered by Winsor & Walford were used, and submitted to an analysis of variance; this technique will now be applied to the present data.

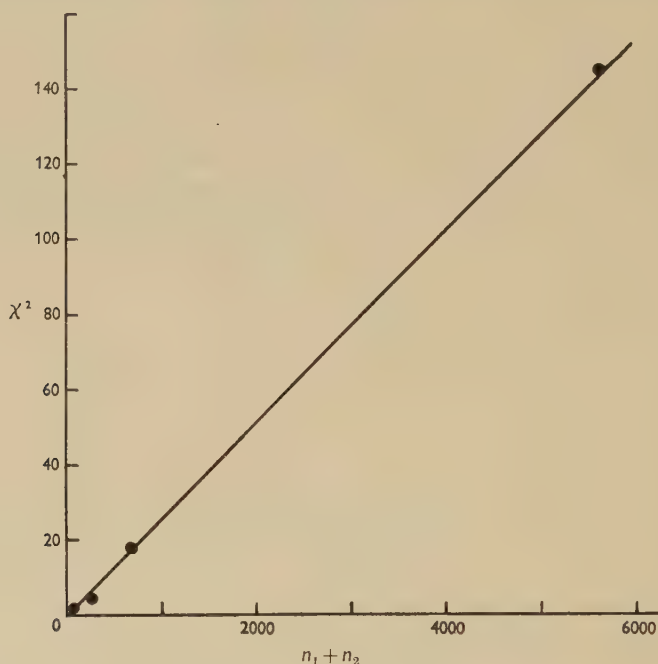


Fig. 2. The relationship between the mean value of χ^2 (grouped values) and the mean catch in paired hauls.

Four of the above six undivided hauls, which have been treated as three pairs, were taken consecutively and these four will be analysed. For the four replicate hauls with eight separate stages of each of the four species counted there are in all 128 observations. (Six results have been neglected because of small numbers.) The results of the analysis can be conveniently tabulated as follows. (Logarithmic values of the catches are used throughout; for details of the theory underlying the method, the paper by Winsor & Clarke (1940) should be consulted.)

The analysis of variance gives the following:

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Hauls (H)	3	0.2255	0.0752
Stages (S)	31	57.3872	1.8512
Interaction:			
H $\times$ S	93	1.2251	0.0132
Totals	127	58.8378	—

The various estimates obtained from the mean squares can be conveniently summarized thus:

(i) The mean square for the interaction is an estimate of σ_{SH}^2 , the 'within haul' variance. Hence $\sigma_{SH}^2 = 0.0132$, standard deviation $= \sigma_{SH} = 0.1149$, and $\log 1.303 = 0.1149$, corresponding to a coefficient of variation of 30.3%.

(ii) σ_H^2 is the 'haul to haul' variance. The mean square for the hauls is an estimate of $32\sigma_H^2 + \sigma_{SH}^2 = 0.0752$. Hence $\sigma_H^2 = 0.0019$, standard deviation $= \sigma_H = 0.0440$, and $\log 1.1070 = 0.0440$, corresponding to a coefficient of variation of 10.7%.

(iii) The variance of a single observation is $\sigma_H^2 + \sigma_{SH}^2 = 0.0151$, standard deviation $= \sqrt{(\sigma_H^2 + \sigma_{SH}^2)} = 0.1228$, and $\log 1.326 = 0.1228$, corresponding to a coefficient of variation of 32.6%.

Winsor & Clarke's results indicated a coefficient of variation of 53% for vertical hauls, and 31% for oblique hauls (n is large), and they suggest that the greater accuracy for oblique hauls is worth further consideration. However, the data now presented show an accuracy for replicate vertical hauls comparable with these authors' value for oblique hauls. It would appear that the greater accuracy of the present series may be ascribed to the more favourable working conditions, viz. a sheltered sea loch in contrast to the less favourable open sea conditions under which Winsor & Clarke's material was collected.

THE DIVIDED HAULS

Throughout the season's work four undivided hauls (bottom to surface) and one divided (bottom to 10 m., 10 m. to surface) haul were taken consecutively, the four undivided hauls being pooled and an aliquot part counted.

A preliminary inspection of the data indicated that as a first approximation the results could be divided into two classes with regard to the discrepancy between the divided and undivided hauls, depending upon whether the animals were mainly above or mainly below the point at which the hauls were broken. The results for those hauls in which the organisms were below the 10 m. level will be considered first.

Animals all below the depth at which the haul was divided.

Since the divided haul is suspect, it is first necessary to examine the assumption that it gives a reliable qualitative estimate of the distribution in relation to the 10 m. level. An inspection of the results indicated that when the organisms were above the 10 m. level the mean total catch of both divided and undivided hauls tended to be similar and under these circumstances, as shown later, they were not significantly different (p. 440). This indicates that no loss is incurred in the 10-0 m. haul. If nothing is caught in the upper 10 m. by the second part of the divided haul it can therefore be assumed that the qualitative information, namely that the animals are all below the 10 m. level, is substantially correct.

The data for *Microcalanus pygmaeus*, no stages of which (except the nauplii) were ever found in significant numbers above the 10 m. level, will first be considered. There were ten different days throughout the season when divided and undivided hauls were taken, and since seven stages were counted there are 140 observations. The results are plotted in Fig. 3 and suggest a loss in the divided haul (compare Fig. 1).

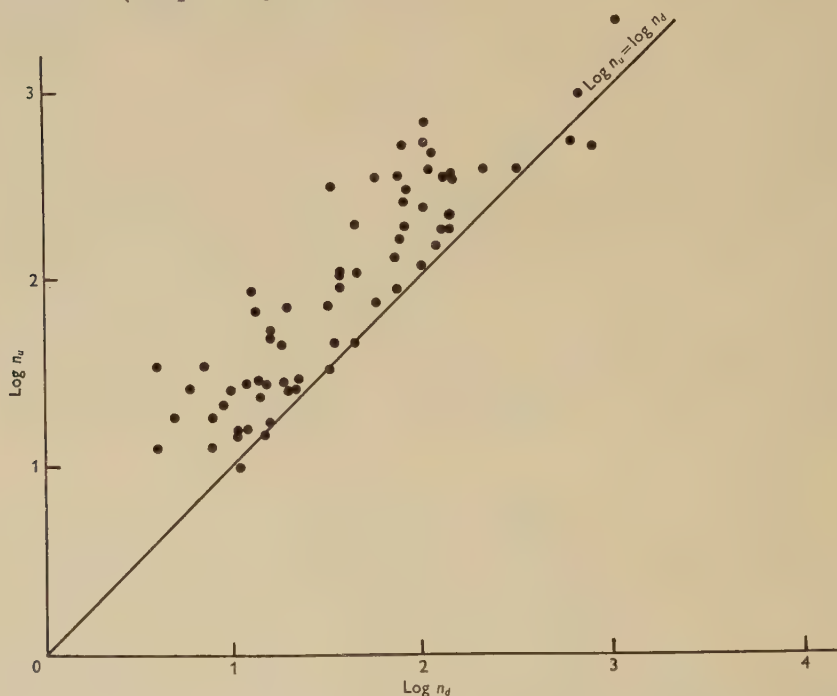


Fig. 3. The relationship (in *Microcalanus pygmaeus*) between catches (log values) for all stages in divided and undivided hauls taken over a season's work when all stages are below point of division of the haul.

The analysis of variance gives the following:

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Stages (S)	6	20.4588	3.4098
Day (D)	9	15.6570	1.7400
Haul (H)	1	4.4500	4.4500
First-order interactions:			
S × D	54	10.0994	0.1870
S × H	6	0.3210	0.0535
D × H	9	0.9230	0.1020
Second-order interaction:			
S × D × H	56	0.8875	0.0164
Totals	139	52.5078	—

It is difficult to assign the day-haul and stage-haul interaction to other than accidental variations, and the values obtained will therefore be added to the second-order interaction to give a residual mean square of 0.0300. The mean square for the hauls can be tested for significance against this value by the z test:

$$z = \frac{1}{2} (\log_e 4.4500 - \log_e 0.0300) \quad n_1 = 1, n_2 = 71, \\ = 2.15.$$

Since the 5% point for z , $n_1 = 1$, $n_2 = \infty$ is 0.6729, the difference between the hauls is significant and the loss in the divided haul indicated by Fig. 3 is significant. It should be pointed out that this is true even though replicate undivided hauls showed a significant difference, since a *set* of hauls is here under consideration. An alternative treatment, which gives the same result, is to consider the divided and undivided hauls on *each* date separately. Associating with the undivided hauls the standard error $\sigma = \sqrt{(\sigma_H^2 + \sigma_{SH}^2)}$ (p. 435) allows for the significant difference between the hauls found previously. Assuming that the divided haul has the same standard error, then the standard error of the difference $n_u - n_d$ is $\sqrt{(2\sigma)}$ and the usual test for significance can be applied.

It is desirable to consider possible reasons for the loss in the divided haul. From the bottom to the 10 m. level the divided and undivided hauls are identical, and since in the hauls under consideration no animals are present above 10 m., it is impossible to escape from the conviction that loss of animals must take place when the net is closed at the 10 m. level in the divided hauls. Two possible causes for this loss may be suggested:

(i) Any organisms still above the throttling gear in the upper part of the net when it is closed will automatically be lost.

(ii) If water is forced upwards from the bottom part of the net when it is closed a further loss of the catch may take place. Three possible mechanisms for such a passage of water upwards may be suggested:

(a) Probably the most important factor is the amount of slack in the throttling cord of the closing mechanism so that when the hauling line is released the net must slow down.

(b) Any deceleration in hauling speed immediately prior to closing the net will, if the net has been moving at a constant speed, tend to force water upwards carrying organisms with it. The person working the winch usually knows when the net is approaching the 10 m. point and may, without realizing it, tend to slow down.

(c) The sudden closing of the net may tend to force a small quantity of water out of the net rather than force it through the meshes.

If in a series of hauls the catch were largely obtained at the same or similar levels then, as a first approximation, all the catch would be expected to be similarly distributed throughout the net and bucket at the time of throttling. Since the loss of water due to the factors outlined above might also be expected

to be similar in a comparable series of hauls, the loss under these circumstances would be proportional to the total catch.

This relationship can be expressed in the form of the regression line of divided and undivided hauls (divided haul being considered as the dependent variable), but since it will be shown that the stages react differently during the season any such relation can only have an average value. The regression line is given by

$$\log n_d = 0.84 \log n_u - 0.03,$$

where n_d and n_u are the numbers in the divided and undivided hauls, respectively. This would mean that for a catch of 100 (n_u), 50% of the animals would be lost in the divided haul.

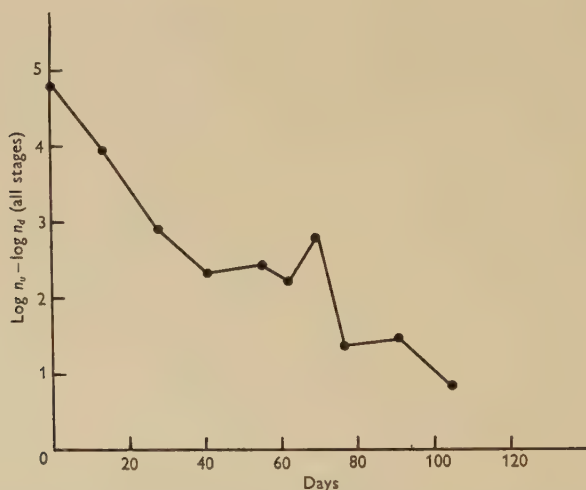


Fig. 4. The ratio of the divided and undivided hauls ($\log n_u - \log n_d$) for total catch, i.e. all stages, plotted against date of catch, showing change in ratio with time.

If the ratio of the catches in the two hauls is plotted against the date of the haul, the figures suggest that the loss changes (in general decreases) throughout the season (Fig. 4).

This is substantiated by analysing the values for the ratio ($\log n_u - \log n_d$) in relation to the date; the analysis of variance gives the following:

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Days (D)	9	1.7625	0.1958
Stages (S)	6	0.0623	0.0104
Interaction:			
D $\times$ S	54	1.5008	0.0278
Totals	69	3.3256	—

The value of the mean square for days is significant, so that the difference between the catches varies significantly with the day on which the catch was taken. The difference does not vary according to the particular stage under consideration. The following is suggested as an explanation of this result. The relation between catch and loss might be expected to depend to some extent on the position in the hauls at which the catch was largely made. If the animals were caught in the same vertical range then the same amount of consolidation (if any) into the receiving vessel and the same distribution throughout the various parts of the net might be expected when the net is closed, so that under similar conditions of water loss on closure, a proportional amount of organisms would be expected to be lost. However, if on certain occasions some of the animals were caught in the deeper layers, they might be expected to be somewhat differently distributed throughout the net and receiving vessel, in general being carried farther down into the lower parts of the net during the later part of the haul. The loss on closure might then be reduced. This explanation would imply vertical migrations of the various stages during the season which is in accord with general observations. If this is true then it indicates that the stages of *M. pygmaeus*, although always below the 10 m. level, do migrate vertically throughout the season. Since the discrepancy between the divided and undivided hauls is less towards the end of the season (see Fig. 4, where $\log n_u - \log n_d$ approaches 0 later in the season), the foregoing agreement would imply a migration to the deeper level during the latter part of the year; such an implication is in agreement with the facts already ascertained for other copepods from such data on their behaviour as are available. It should be possible to relate these changes to the factors which control seasonal vertical migration, but the available information is inadequate. An inspection of the data in relation to temperature which might be expected to affect such migration gives no significant correlation. However, changes in the order of the discrepancy were most marked when there were sudden changes in temperature.

It should be pointed out that this change in the relationship between the divided and undivided haul throughout the season could conceivably be explained by some gradual change in technique; this explanation is hardly adequate.

This loss of catch with vertical divided hauls does not appear to be peculiar to the present series of observations. Thus Kemp, Hardy & Mackintosh (1929) and also Marr (1938) draw attention to the discrepancy between 'open' and 'closed' horizontal hauls using the same net, the 'closed' haul always yielding a comparatively poor catch. They suggest that the 'open' horizontal haul possibly gives a fictitious result owing to catching animals whilst hauling in the net. The loss of catch in the 'closed' haul as a result of the tendency of the net to fall backwards could have contributed materially to the discrepancy, since it would lead to losses in the 'closed' haul.

Wiborg (1948) has recently published a detailed account of a comparison of several methods of taking vertical and oblique hauls and an inspection of his Table IV indicates a loss with the vertical closing net. Some of his results are grouped together and shown in summary form in Table IV. The figures for the Clarke-Bumpus sampler (P.S.-8) are organisms per 1000 l., while those for the closing net (8/72) are the total catch. If the net is behaving in a similar manner throughout each haul it would be expected that the ratio of the

TABLE IV

	25-0		50-25		100-50		150-100	
	P.S.-8	8/72	P.S.-8	8/72	P.S.-8	8/72	P.S.-8	8/72
<i>Calanus finmarchicus</i> :								
Copepodites and adults	4188	21183	306	2216	117	194	46	138
Nauplii and eggs	4303	6900	4769	4609	214	60	122	25
<i>Calanus hyperboreus</i> :								
Copepodites and adults	109	422	54	76	26	14	1	51
Nauplii and eggs	94	500	53	—	—	—	—	—
Other organisms than copepods	598	1942	833	338	186	178	23	58

Clarke-Bumpus sampler catch to the net catch would be approximately constant, an assumption which is independent of the absolute filtration coefficient of the net. Although the species and stages do not behave in an identical way it is clear from the figures that the ratio (sampler/net) is usually much lower in the 0-25 m. haul than the deeper hauls. Since it may be presumed that the 0-25 m. hauls were made without closing the net it would appear that the lower ratio for this section of the haul is due to not closing the net and that the catches in the other divided net hauls are lower as a result of losses on closing the net.

Hauls in which all the organisms were above 10 m.

Since it has been shown that in general, in the divided haul, there is a loss of organisms caught below 10 m. it is again necessary to examine the possibility that the qualitative division is correct. In the hauls under consideration no animals were caught below 10 m. in the divided haul; a small number may have been lost but these may be neglected if there are moderate numbers above 10 m. Both the divided and undivided hauls can, therefore, be considered as catching animals only between 10 m. and the surface.

The results for *Centropages hamatus* have been used, since on three occasions six of the stages were all above the 10 m. level on three different days during the season. The analysis of variance gives the results as shown on p. 441.

The day-haul and haul-stage can again be combined with the second-order interaction to give a residual mean square of 0.074.

The difference between the hauls is not significant so that the divided and undivided hauls do not differ significantly when all the organisms are caught above the 10 m. level in the two hauls.

The coefficient of variation of a single observation can be obtained from the residual variance which is an estimate of

$$\sigma_R^2 = 0.074.$$

Hence the standard deviation = 0.272, $\log 1.871 = 0.272$, corresponding to a coefficient of variation of 87%.

Analysis of variance

Source of variation	Degrees of freedom	Sum of squares	Mean square
Main effects:			
Days (D)	2	0.701	0.351
Hauls (H)	1	0.063	0.063
Stages (S)	5	1.221	0.244
First-order interactions:			
D × H	2	0.116	0.058
D × S	5	0.703	0.141
H × S	10	1.784	0.178
Second-order interaction:			
D × H × S	10	0.431	0.043
Totals	35	5.019	—

It is evident that the estimate of the population of these short 10 m. hauls is very much less accurate than that obtained in the long hauls previously discussed.

Several sources of error in these short hauls may be suggested. Any error in measurement of the 10 m. depth either by inaccurate adjustment of the metre wheel, or any subsequent slip in the friction drive, whilst having little effect when the animals are being caught in a 0–60 m. haul, would considerably affect the catch when it is being taken through a 10 m. haul, taking only 20 sec.; an error of ± 1.0 m. would affect the volume sampled by $\pm 10\%$. Further, the net may not begin to fish efficiently immediately winding commences; the winder may, in releasing the winch catch, drop the net a small distance, and constant speed may not be attained for some seconds.

Hauls with animals above and below 10 m.

These are subject to all the errors discussed above, and the resultant effect will be determined by the proportions of the population above and below the level at which the haul is broken. If the animals are largely above this level the estimate of the population will be a poor one with no significant difference between divided and undivided. As the animals are found in greater proportion below the dividing level the error due to losses on closing the net will become more important. It is possible to apply an overall correction factor to the lower section of the haul, but in view of the change of reaction with time of the various stages it can hardly be considered satisfactory. Further analysis of the data does not appear, therefore, to be profitable, but the above may be illustrated by plotting the ratio between the undivided and the divided hauls ($\log n_u - \log n_d$) against the percentage in the upper 10 m. of the haul. The

results for the first part of the season's hauls on *C. hamatus* are shown in Fig. 5. If the hauls were identical the points would lie on the line $\log n_u - \log n_d = 0$, but the loss ($\log n_u - \log n_d$ positive) increases as the population of the animals below the 10 m. level increases.

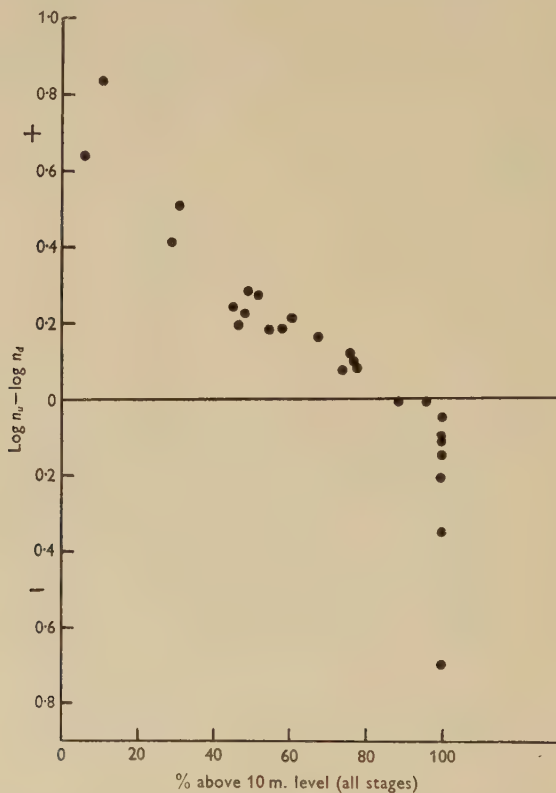


Fig. 5. Change in ratio of divided and undivided hauls (in *Centropages hamatus*) as the population is found in greater proportion below the point of division of the haul.

THE EXPERIMENTAL DATA

It has been indicated that there are losses in a divided haul when the net is closed by a throttling cord, and it has been suggested that this is largely due to deceleration with a consequent loss of water from the net and that this water carries organisms with it. The sequence of events on throttling can be illustrated by reference to the Discovery net whose dimensions are given in full detail by Kemp *et al.* (1929).

The net has 3 ft. bridles on a 50 cm. diameter mouth and between the mouth and the filtering surface is a canvas cylinder whose depth to the closing rings is 23 in., i.e. a total length of 57 in. from the release gear to the throttling band.

The total length of the throttling cord doubled is $16\frac{1}{2}$ ft. The drop on closing, if the net were stationary, would be the difference between 57 in. and 99 in.—say $3\frac{1}{2}$ ft. Of this drop about 1 ft. takes place before closing starts and a further $2\frac{1}{2}$ ft. during closing. It should be emphasized that some slack is necessary in the throttling cord for normal working of the closing mechanism, particularly under adverse conditions, but if the throttling line were tight between the attachment to the release and throttling loops, there would be negligible fall before the closing started and the half of the circumference of the circle, 31 in., as the rope tightened.

In the case of a net which is being hauled vertically there will be a tendency for it to continue to move upwards after being released from the hauling line owing to its own momentum, and the resultant movement of the net will

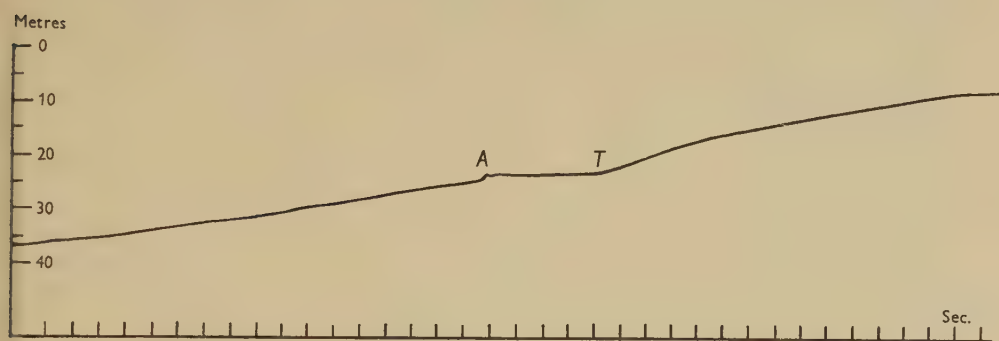


Fig. 6. Copy of the tracing of a depth record; constant speed to *A*, at which point messenger engaged, the weight coming on to throttling line at *T*. Horizontal scale in seconds; vertical scale in metres with an arbitrary zero.

depend upon the speed of hauling and the weight attached to the net. If the net remained stationary after release of the hauling rope, then at a hauling speed of 0.5 m./sec. it would be approximately 2 sec. before the weight came on the throttling line again. A record of the changes in position of a net on closing was obtained by attaching a small depth recorder to the bucket of the net. The net was handled by a mechanical winch in order to obtain a uniform hauling speed and the conditions were chosen so that there was as little movement of the ship as possible. Further, in order to exaggerate the effect about 1 ft. extra throttling rope was used. Fig. 6 is copied from a photograph of the record. No actual fall of the net is shown but after the messenger engages (at *A*), the net remains virtually at the same level until caught up again (at *T*) by the throttling rope.

That the slowing down of the net causes water to be ejected from the net was confirmed by taking a film using a model net.¹ The net was a scale model, one-

¹ This and a number of other films were taken by Mr F. M. Marshall, and his expert assistance is gratefully acknowledged.

fifth of the Discovery net, without the canvas top. In view of the difficulties of working vertically, a horizontal tow was made, using an electric motor to obtain uniform speed. Inside the opening of the net was fastened a coarse mesh bag containing finely powdered potassium permanganate. The effect of closing the net was imitated by stopping the motor and reducing the forward speed by a line attached to the tail of the net. Part of the film is shown in Pl. I. The film was taken at a speed of 64 frames/sec., and the ejection of water when the net is stopped can be clearly seen.

DISCUSSION AND SUMMARY

The analysis of data on replicate vertical plankton hauls gives a value of the order of 35% for the coefficient of variation of a single observation for a haul of moderate length. The results are similar to those presented by Winsor & Walford (1936), and Winsor & Clarke (1940); and are not at variance with the suggestion that the animals are randomly distributed, and that the variations obtained are largely dependent upon variation in the volume of water filtered by the net.

When short hauls are taken, as is done when information is sought on the plankton of a limited vertical column, then the coefficient of variation of a single observation is of the order of 90%. It is suggested that this is due to an accumulation of small errors of technique which weight the result heavily when only a small column of water is filtered. For examination of such short columns oblique or horizontal hauls should be given consideration.

It is shown that in divided hauls in which the net is closed on the Nansen principle losses in catch take place and it would be advisable to abandon its use in quantitative plankton work. The alternative seems to be an apparatus such as the Clarke-Bumpus sampler (Clarke & Bumpus, 1940), or a Kofoid-type net for horizontal hauls (Kofoid, 1912).

Any mechanism which, as a result of its closing action, results in a tendency for the net to fall will cause a loss in the catch, although the presence of a cone and a small opening would tend to reduce this loss (Kofoid, 1911).

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EXPLANATION OF PLATES

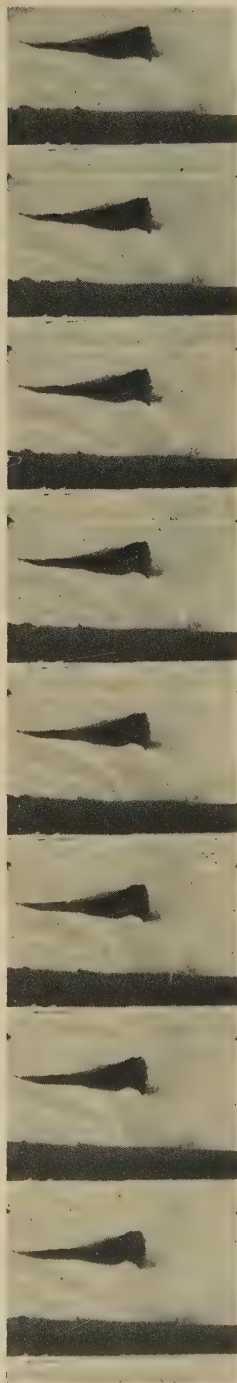
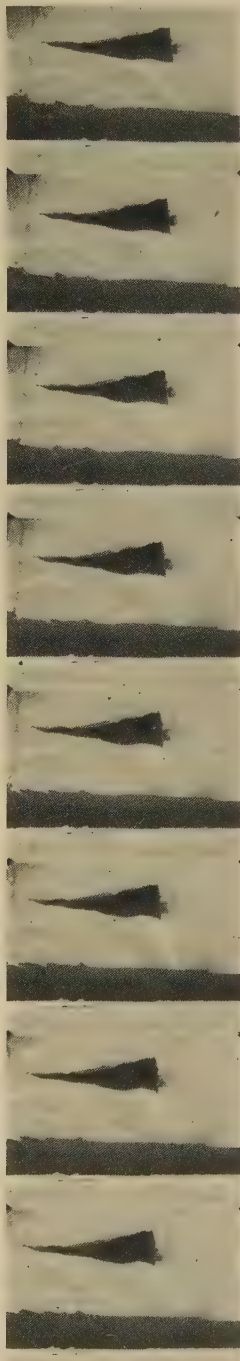
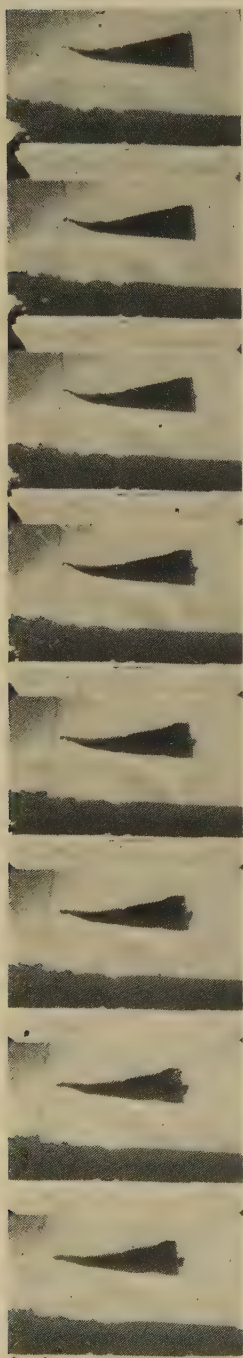
PLATE I

Photograph of escape of material from net on stopping (consecutive frames from top left to bottom right). The film was taken at 64 frames/sec. and the speed of towing was approximately 0.5 m./sec. Hauling was stopped at the 3rd frame (A).

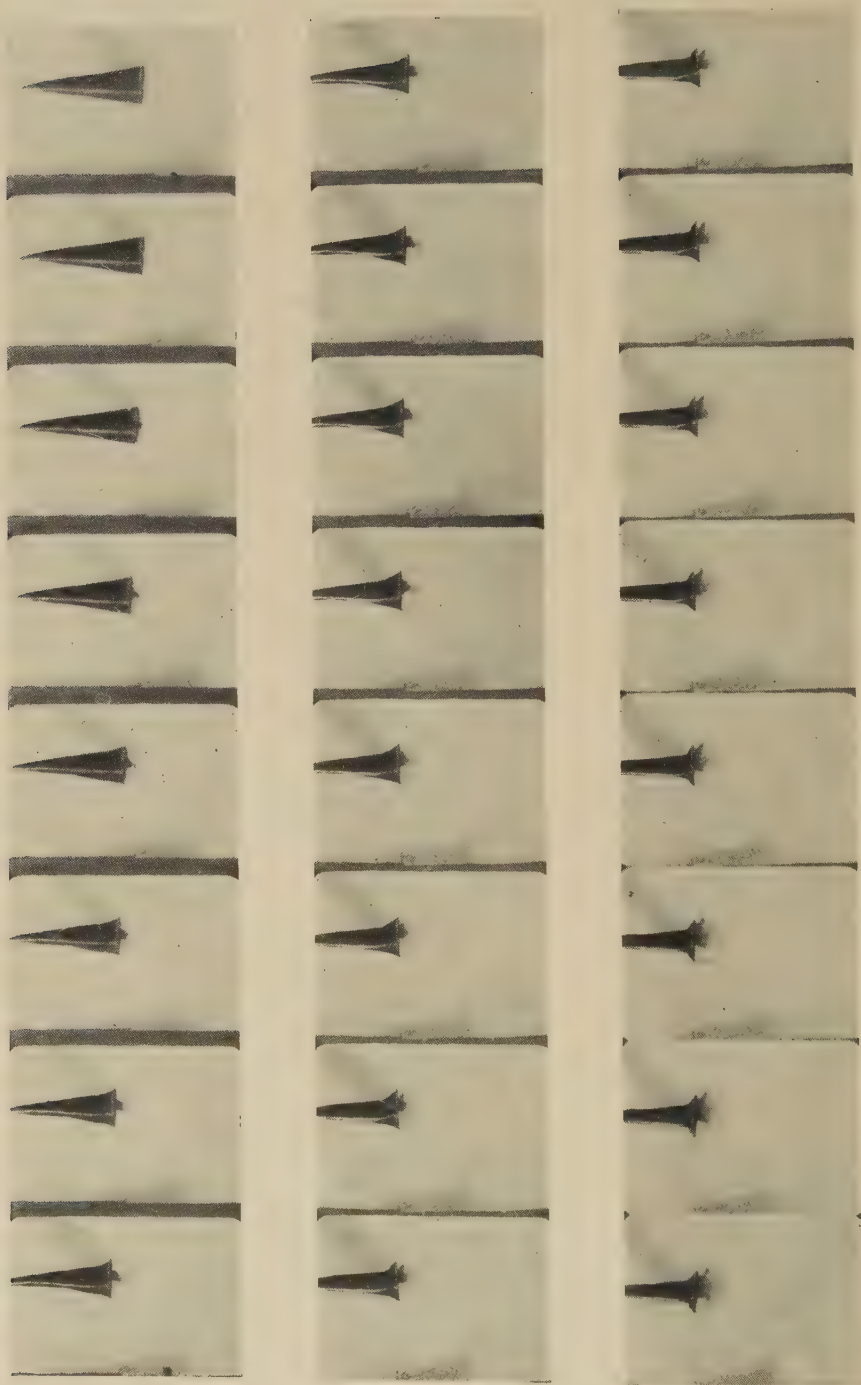
PLATE II

Another photographic record of material escaping from the net (consecutive frames from top left to bottom right). Hauling was stopped at the 3rd frame (A).

A



A



RESPIRATORY MOVEMENTS OF *ARENICOLA MARINA* L.: INTERMITTENT IRRIGATION OF THE TUBE, AND INTERMITTENT AERIAL RESPIRATION

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(Text-figs. 1-9)

Van Dam (1937, 1938) studied the respiratory movements of lugworms (*Arenicola marina* L.) in glass tubes. He found that they propelled water through the tubes by means of wave-movements running along the body, usually from tail to head, and that 'ventilation was intermittent; ventilation pauses alternated, sometimes very regularly, with ventilation periods; in some cases the pauses lasted as long as 40 minutes'. In the following paper, the mechanism and biological significance of this intermittence are investigated. The worms were studied in glass U-tubes. It will be shown, in another paper, that very similar behaviour occurs in the burrow, in sand.

APPARATUS FOR STUDYING INTERMITTENT IRRIGATION

Van Dam observed the worms visually, and measured the volumes of water pumped by collecting the output in a graduated cylinder. The period of time over which a worm can be studied in this way is necessarily rather limited. With the apparatus shown in Fig. 1, the behaviour of a worm can be continuously recorded on smoked paper for 2 or 3 days, and a rough idea of the volumes pumped can be got from the records.

The worm lies in a U-tube (of internal diameter 0.75 cm.). Each limb of the U is connected with a T-piece whose lower end is constricted, to discourage the worm from creeping farther upwards. The upper end of the T-piece communicates, through a 20 c.c. pipette bulb, with a wide cylinder (internal diameter 3 cm.). The side arm of the T-piece leads through a T-tap to the same cylinder. The side arms of the taps are connected by a capillary (bore about 0.15 cm.). The whole apparatus is filled with sea water. One of the wide cylinders contains an aeration jet. The other contains a paraffin float, connected with an isotonic lever writing on a slowly moving kymograph. The time trace is provided by a clock whose minute hand is bent forward and connected to a lever with a frontal writing point. This traces an approximation to a sine curve at 1 cycle per hr.

Most of the observations were made with the taps turned as shown in the figure. When this is so, the worm can circulate water along the U, through the 20 c.c. bulbs and wide cylinders and the capillary. Thus it can get a supply of freshly aerated water. Owing to the resistance of the capillary, any such pumping results in slight variations of level in the wide cylinders and will therefore be recorded on the drum. Rather different conditions arise if the taps are turned through 180° ; these will be dealt with later.

The worm's output can be estimated as follows. The lever magnification was about 12. The capillary passed 6.7 c.c./min. at a pressure of 1 cm. sea water. Hence the flow rate through the capillary is $1.1 d$ c.c./min., where d cm. is the displacement of the writing point from the zero position. The paper moved at 2.4 cm./hr. Hence the volume flowing through the capillary during any period is $27.5 a$ c.c., where a cm.² is the area between the tracing and the zero line. It must be borne in mind that the flow-rate through the U-tube is not necessarily the same as that through the capillary, owing to variation in the amount of water in the wide cylinders. A 1 cm. excursion of the writing point means a transfer of 0.6 c.c. of water from one cylinder to the other; if the writing point is moving away from the zero line, the flow-rate through the U-tube exceeds that through the capillary, and if the lever is moving towards zero the opposite condition holds.

The experiments lasted for many hours, and sometimes for 2 or 3 days. They were set up in an unheated room, where the temperature varied (over the whole period of experimentation) from about 8° to 14° C.; in the course of a single experiment the variation was seldom more than 1 or 2 degrees. To avoid unnecessary stimulation of the worms, nobody but the writer, or visitors in

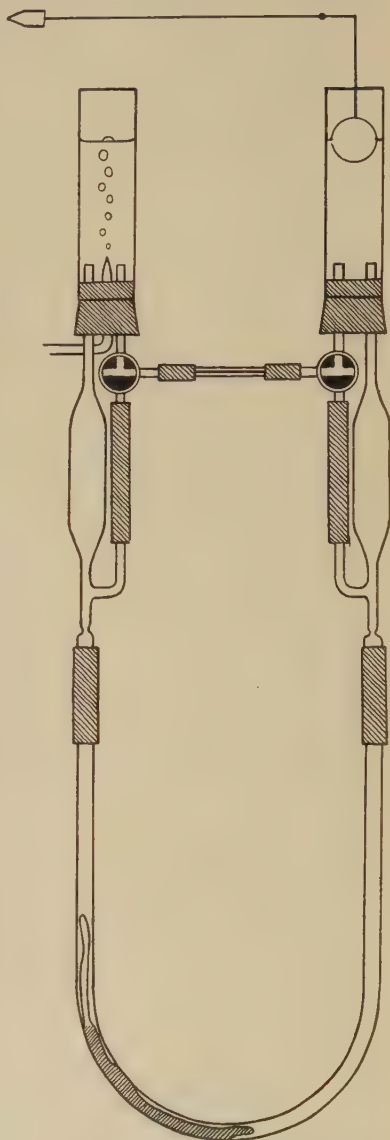


Fig. 1. Apparatus for recording the irrigation cycles (see text).

his company, ever entered the room; and, as it was necessary to interpret the records by watching the worms from time to time, the electric light was kept continuously on. Daylight was excluded.

IRRIGATION AND LOCOMOTION

The worms can displace the water in the U in several different ways, and before considering the records obtained, the characteristics of these various kinds of movement must be summarized. For further details, the works of Just (1924) and van Dam (1938) may be consulted. The movements depend on waves travelling along the whole length of the body, except the first three or four segments and the tail.

Irrigation. The worm lies in the tube, with its ventral and ventro-lateral surfaces pressed against the glass wall, but with a space (containing the gills) between the dorsal surface and the tube. Waves of swelling, which completely occlude this space, move steadily along the body and thus drive water through the tube. The waves generally run in a headward direction, but tailward waves are sometimes seen. It is of course obvious that in irrigation the direction of the water stream coincides with that of the waves.

Antikinetic locomotion. In this case the direction in which the worm creeps is opposite to that in which the waves traverse the body. The body as a whole is elongated, and at most points clear of the tube. Waves of swelling run along the body and occlude and grip the tube. The waves act as fixed points, and the worm as a whole travels, driving water before it. Headward waves result in tailward locomotion and a tailward displacement of water, while tailward waves have the opposite effects. In either case, the notopodia are so oriented as to assist the movement by preventing any backsliding. Antikinetic locomotion can be very vigorous and swift, though it is not always so.

Synkinetic locomotion. In this case, the worm creeps in the direction of wave-travel. One often sees that a worm, which is vigorously irrigating in a headward direction, creeps gently headwards at the same time. The mechanism of this movement, which is never very swift, is obscure; perhaps the orientation of the noto- and neuropodia plays a decisive part. The water in the tube is propelled headwards, because the irrigation waves move much more rapidly than the worm as a whole. Theoretically, as all the movements appear to be reversible, a worm could creep gently tailward during tailward irrigation; but this has not been noticed, either by Just (1924) or by myself.

The most fundamental point, physiologically, seems to be the direction of wave-travel along the body. Headward waves can result in headward irrigation, more or less vigorous tailward locomotion, or gentle headward locomotion, and all of these variations merge into, and can smoothly change into, each other. On the other hand, a process involving headward waves only changes into one involving tailward waves after a definite pause, as if the two performances were quite distinct and incompatible.

DESCRIPTION OF THE IRRIGATION CYCLES

When newly put into the apparatus the worm is restless and its behaviour is unpredictable. Periods of similar restlessness may suddenly set in at other times; for instance, by narrowing itself and burrowing, so to speak, along its own ventral surface, a worm can easily reverse itself in a tube which, at other times, it seems comfortably to fill; sometimes this happens, after which, of course, the writing on the drum appears the other way up.¹ Or a worm may spoil a good record by 'running amok' and forcing itself through the

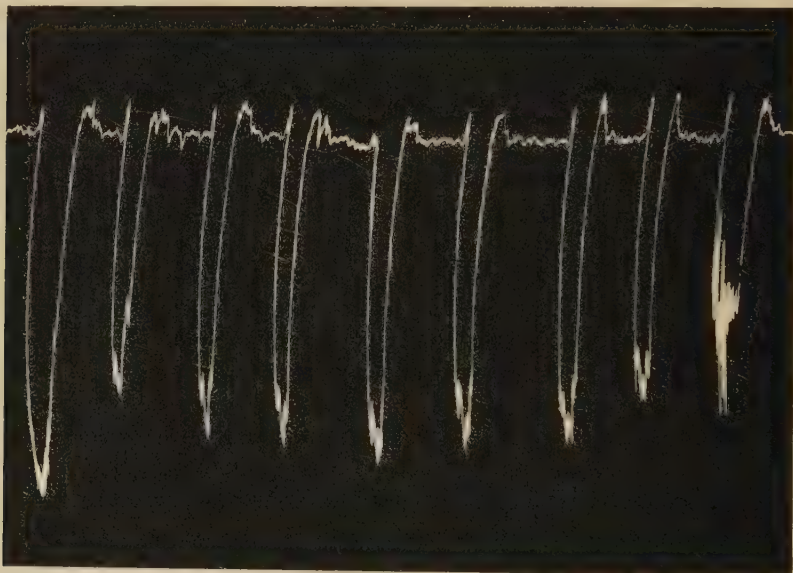


Fig. 2. Three-phase irrigation cycles, traced by a worm with its head towards the float. (Worm O 7.) Duration of printed extract 4 hr. 20 min. *In all records:* Read from left to right.

narrow constriction into one of the 20 c.c. bulbs. Generally, however, the animals settle down and show outbursts of irrigation alternating with rest periods, the cycle continuing—often for 12 hr. or so—with almost clock-like regularity.

The cycles, as traced on the record, vary somewhat in timing and in appearance from worm to worm, and, in the same worm, from day to day. Nevertheless, there is an underlying three-phase pattern, to which the outbursts always conform.

The essential features of this pattern can be seen in Fig. 2. In the relatively quiet intervals between outbursts, the worm was lying in the curved part of the

¹ To avoid confusion, the extracts in the illustrations are chosen so that the worm's head is always towards the float. This means that a headward movement of water causes a downstroke of the writing point.

U, with its head towards the float and its body rather short and thick; it showed occasional slight movements, for example of the head and proboscis. At the beginning of each outburst it lengthened and waves began to travel headwards along its body. These resulted first in tailward locomotion, causing a short rise of the lever (phase 1). But soon the locomotion passed over into headward irrigation—a change brought about by an alteration of attitude, but not of the direction of wave-travel—and as this happened, the lever plunged down (phase 2). After a period of vigorous irrigation, during which the worm crept very gently back to about its original position, the waves slowed up and stopped. There followed a 'rebound' period, when the worm irrigated in the reverse direction, i.e. with tailward waves (phase 3). This gave a second, more prolonged rise of the lever. After this the worm became quiescent.

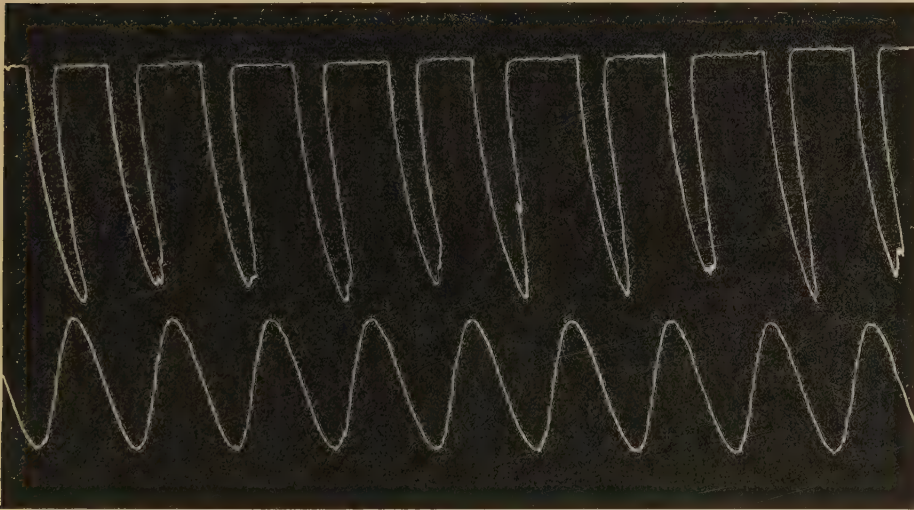


Fig. 3. Irrigation cycles in which the first and third phases are inconspicuous. Worm with head to float. (Worm O 49.) Time trace at 1 cycle per hr.

The second of the three phases—that of headward irrigation—is always the chief one, as long as the taps are turned as shown in Fig. 1. The others are more variable. The final 'rebound' phase may consist only of one or two very slow waves, taking place while the lever returns from the second phase and therefore leaving no trace on the record. Again, the backward locomotion in the first phase varies greatly in intensity. The worm of Fig. 3 gave only very slight, occasional tailward creeps, and only the faintest 'rebounds'. This is probably how the worms used by van Dam (1938) were behaving, as he makes no mention of the triphasic nature of the outbursts. The first part of Fig. 5 is particularly interesting because, as will be shown in another paper, it corresponds closely with the worm's normal behaviour on the beach. In this case, the

tailward locomotion phase is always well-marked. Starting from the bottom of the U, the worm crept up, at each outburst, until its tail had passed through the T-piece and extended for 1 cm. or so into the 20 c.c. bulb. Then, during the irrigation phase, it crept gently down again. The 'rebound' phase was vestigial, as the record shows.

In rough figures, the worm in Fig. 2 pumped about 20 c.c. of water at each burst, and the flow-rate through the capillary at the peaks was about 4.5 c.c./min. Corresponding figures for the other worms whose tracings are illustrated are: Fig. 3, 80 c.c., 6 c.c./min.; Fig. 5, 40 c.c., 7 c.c./min. The internal volume of the U-tube was 25 c.c., of which the worms occupied at least 5 c.c. It will be seen that the worms renewed all the water in the U-tube respectively once, four times and twice at each burst.

IS INTERMITTENCE SPONTANEOUS OR REFLEX?

The obvious explanation of intermittent irrigation is the reflex one. As the worm lies quietly in the tube, oxygen disappears and end-products accumulate. Presently, as we may suppose, the changes stimulate rhythmic activity, which ceases again when new water has been brought and the irritating conditions are removed. One should, however, be cautious in adopting explanations of this type. Isolated strip preparations from polychaetes often show periods of rhythmic activity alternating with periods of rest, so the intermittence may be spontaneous—i.e. produced solely by processes internal to the worm (Wells, 1939).

In the present case, there is little doubt that the intermittence is truly spontaneous, as the following evidence shows.

(i) If one pins out a worm with two pins near the front end and two at the base of the tail (being careful to avoid injury to the nerve cord) and records its movements by means of a glass hook passing under the middle of the body (Fig. 4), one often gets outbursts of activity, continuing very regularly, hour after hour, with about the same period as that of the irrigation outbursts. Now, the record in Fig. 4 is part of a very regular series of outbursts, which lasted for 13 hr. It was traced by a worm pinned to a weighted sheet of cork in a wide, shallow dish of sea water; the water was aerated and stirred by an air jet. One can hardly suppose in this case that the onset of each burst of activity is due to chemical conditions arising in the neighbourhood of the worm, and its cessation to the bringing of new water by the movements. This experiment shows that there is a 'clock' of some kind in the worm, of about the right frequency to account for the irrigation outbursts.

(ii) Van Dam (1938) found that the pauses did not disappear, or even shorten, when the oxygen content of the water was reduced by bubbling nitrogen through it. There was, however, a great increase in the amount of water pumped if the worms were given well-oxygenated water after a period

of oxygen lack. These experiments tend to exclude oxygen exhaustion as a possible stimulus for the outbursts, though they do not exclude the accumulation of CO_2 or other end-products.

(iii) The aerating effect of irrigation can be greatly reduced by turning the taps through 180° from the position shown in Fig. 1. The worm can still circulate the water and any such pumping will be recorded on the drum as before—but, as the water no longer circulates through the 20 c.c. bulbs and the wide cylinders, it can no longer be aerated. There is, in fact, a slight ebb and flow between the cylinders, corresponding with the excursions of the

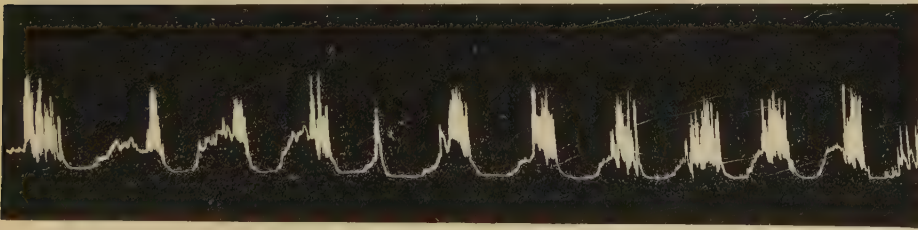
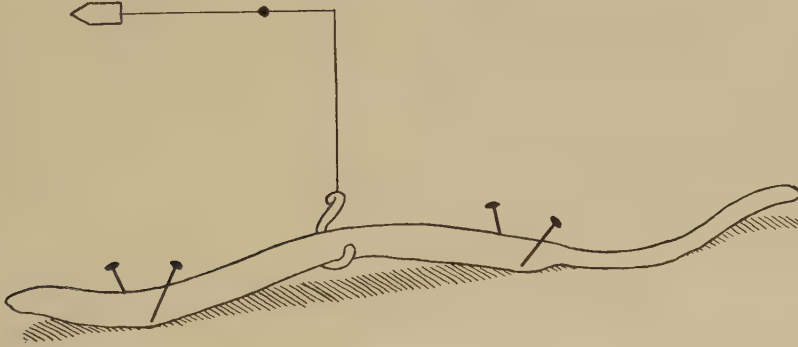


Fig. 4. *Above:* worm pinned to a cork sheet, on the bottom of a flat dish. *Below:* record traced by the same. Duration of printed extract, 7 hr.

lever; but, as this consists of 2 or 3 c.c. of water at most, moving to and fro quite slowly, its aerating effect is negligible compared with that of the circulation before reversal of the taps. The bulbs were included to reduce this effect. The worms were occasionally seen to extend about 1–2 cm. of their tails into the 20 c.c. bulbs, but it is hardly likely that they could get much oxygen, or dispose of much CO_2 , by this means.

If now the outbursts are reflexly produced, they should be prolonged and intensified when the taps are reversed. But nothing of the sort occurs. Fig. 5 shows a typical result; the taps were turned at X (the float was lifted out of the water and dropped again, to mark this moment on the record). The

outbursts continue; their frequency is slightly raised (but in other worms it was unaltered, or even lowered); and, though the tailward excursions continue, the phase of headward irrigation is diminished and sometimes fails to appear on the record at all.

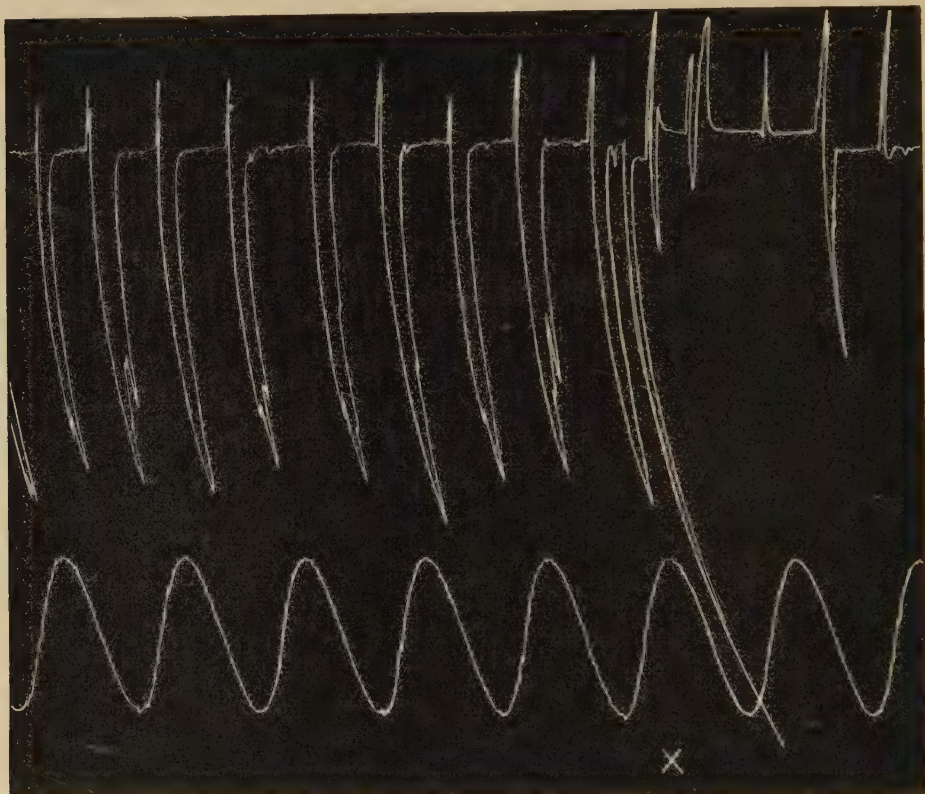


Fig. 5. Worm with its head to the float. At X, the taps are turned to 'no air'. (Worm O 48.) Time trace at 1 cycle per hr.

Fig. 6 shows the effect of turning the taps back to 'air' again, after a 7 hr. period of 'no air'. This worm had previously traced the record of Fig. 3. In the first part of Fig. 6, with the taps at 'no air', it was tracing outbursts at about the same frequency, but with much less voluminous irrigation. At the moment of turning the taps, there was a short spell of gentle headward, then tailward irrigation; this was probably a response to slight vibration of the apparatus caused by the handling of the taps. Then, when the next outburst fell due, the worm crept nearly to the T-piece, and began headward irrigation. It was not until this moment, that the aerated water first reached the worm. The response was very marked. Previously, the worm's movements had been

rather feeble and jerky, and its whole appearance suggested weakness and even injury by the 'no air' conditions; but now it suddenly revived and became alert and vigorous; and it began a burst of exceptionally powerful headward irrigation which lasted for 40 min. (total volume pumped 240 c.c., peak flow rate through capillary 8.25 c.c./min.). After this, the time intervals between outbursts were at first very short, and gradually lengthened out; but, even after the taps had been turned to 'air' for 10 hr., the rhythm was still quicker than at the beginning of the experiment (Fig. 3). As, however, the worm had been in the apparatus by this time for about 40 hr., an exact agreement is hardly to be expected.

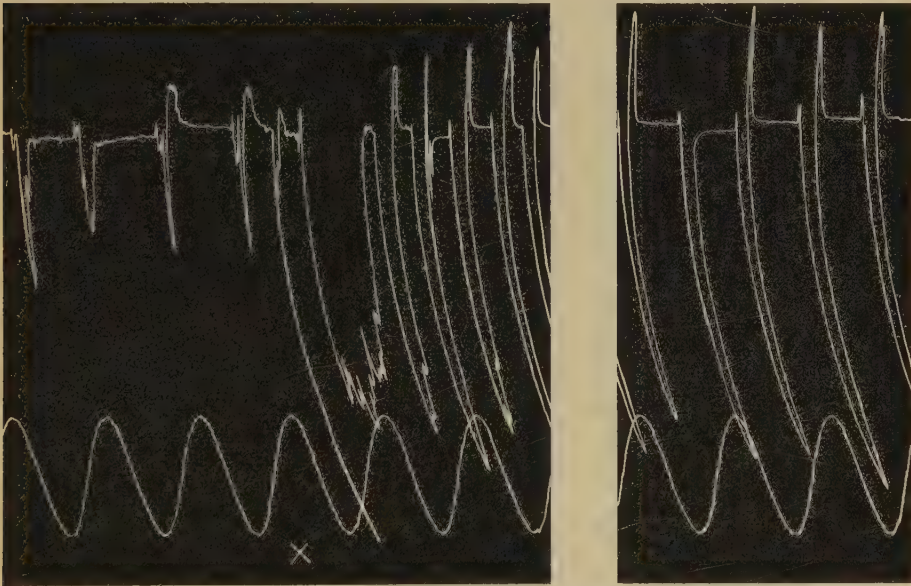


Fig. 6. Worm with its head to the float. The first extract begins with the taps in the 'no air' position. They are turned to 'air' at X. The second extract begins (still with the taps at 'air'), 3 hr. after the end of the first. (Worm O 49.) Time trace at 1 cycle per hr.

These results show that the cycles can be greatly modified, in amplitude, duration and frequency, by external conditions; but all the evidence tends to the conclusion that the intermittence itself is an inherent property of the worm. The case is analogous to that of the heart beat; rhythmicity is an inherent feature of the heart's organization, though the details of the rhythm can be modified by the vagus and sympathetic nerves.

LOCATION OF THE PACEMAKER

Wu (1939) studied the action of drugs on longitudinal body-wall strips from *Lumbricus* and *Arenicola*. He wrote: 'In contrast to the earthworm strips, those of *Arenicola* showed spontaneous activity only if the ventral cord was

present. The ventral strips were very active and often showed outbursts of rhythmic activity alternating with more quiet periods.'

To see whether the intermittent activity of isolated, innervated body-wall strips was at all comparable with the irrigation cycles, I made a series of experiments in the following way. The head, together with the first three chaetigerous segments, was removed by means of a transverse cut with a safety-razor blade. The tail, and the last two chaetigerous segments, were similarly removed. The middle part—of fourteen segments—was opened along

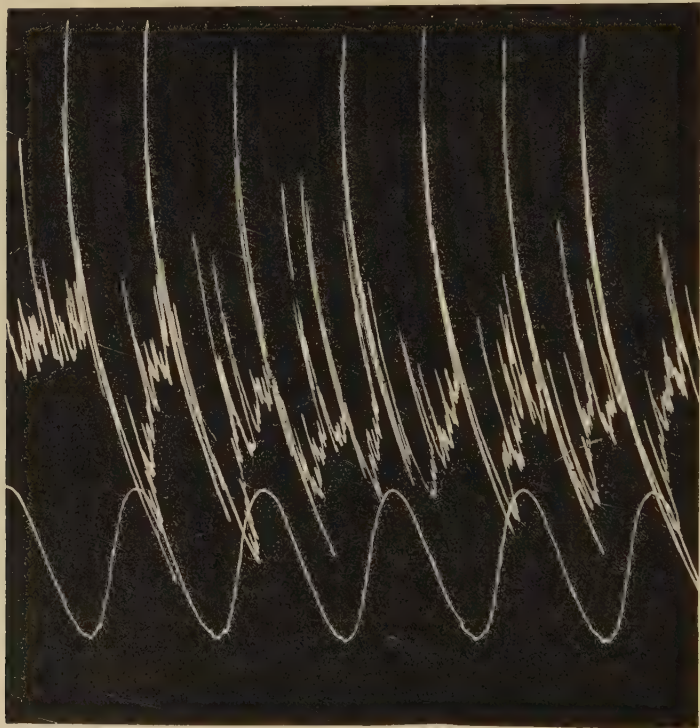


Fig. 7. Record traced by a body-wall strip, including the nerve cord, from the middle region of the body. Upstroke of lever means contraction of preparation. Time trace at 1 cycle per hr.

the mid-dorsal line, and the gut was removed. The body wall was then tied at both ends and suspended as a longitudinal preparation, in a large vessel of briskly aerated sea water, and connected to a light isotonic lever.

The resulting preparations showed continuous, rather irregular rhythmic activity, but one can generally see, on the tracings, bursts of outstanding vigour appearing at more or less regular intervals, with about the same timing as that of the irrigation cycles. Sometimes these were very evenly spaced, for several hours on end, as in Fig. 7.

In view of these results, and of Wu's observation that spontaneous activity occurs only in the presence of the ventral cord, one may reasonably place the pacemaker for the irrigation cycle, tentatively at least, in the nerve cord itself. The presence of the brain seems quite unnecessary.

INTERMITTENT AERIAL RESPIRATION

At high tide, the lugworm can get plenty of oxygen by circulating the water in its burrow. If, however, the tide recedes, leaving the surface dry and stagnant water in the lower part of the burrow, circulation is no longer possible and serious oxygen shortage could result. During an earlier study (Wells, 1945), I placed lugworms in glass U-tubes partly filled with sea water, which they were unable to circulate, and saw on several occasions what is evidently a method of aerial respiration. The worms crept backwards to the surface of the water, and drew air between their dorsal surfaces and the tube, so that it came in contact with the gills. This process might evidently be brought about by means of an adaptation of the irrigation cycle. The phase of tailward locomotion would bring the worm to the water surface and the following headward irrigation would then draw air down to the gills. If so, aerial respiration will be intermittent; and the experiments now to be described were made to find out whether this guess is true.

The apparatus was simple (Fig. 8). The worm was placed in the same U-tube as before, but now only partly filled with sea water. One end of the U was connected with pressure tubing to a float-recording device, so that the oscillations of the level in the U were written on the kymograph. For most of the time, the worms were left to write their own stories, but occasionally they were visited to see what they were doing, and once or twice they were watched continuously for an hour or so, and their behaviour was noted minute by minute.

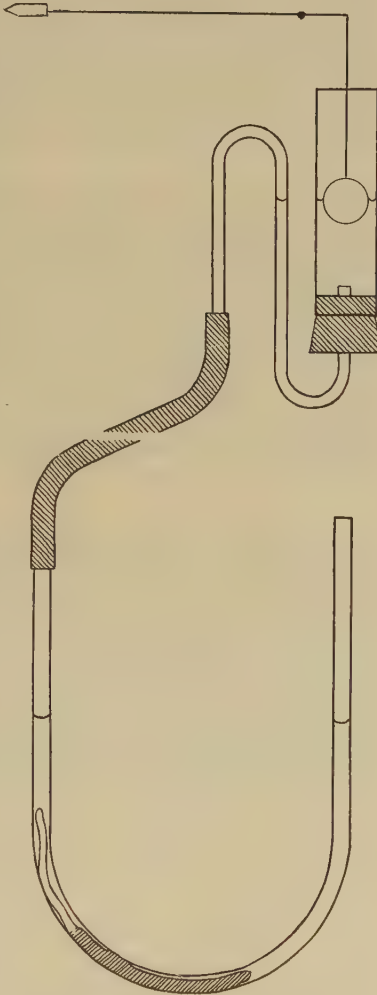


Fig. 8. Apparatus for recording aerial respiration (see text).

Parts of the tracings show confused, unanalysable activity, but usually the records are obviously periodic. The timing of the cycles varies considerably, as may be illustrated by the record of worm T 6 (Fig. 9). The worm was continuously watched during the last 2 hr. of the third extract, and its behaviour

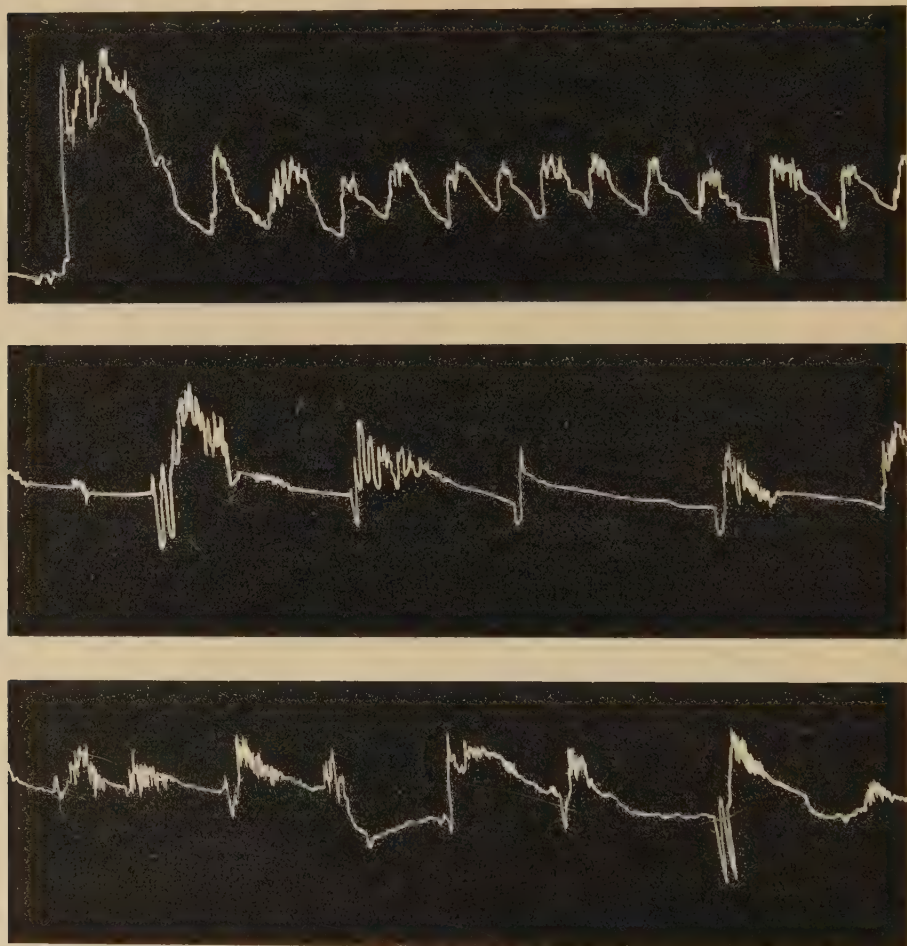


Fig. 9. Three extracts from the record of worm T 6. The worm was put in the apparatus of Fig. 8 at 15.46 hr., 29 December 1948. The three extracts start respectively at 19.00 hr., 29 December 1948; at 02.00 hr., 30 December 1948; and at 13.00 hr., 30 December 1948. Duration of each extract, $5\frac{1}{2}$ hr.

was as follows. During the quieter parts of the record it was lying, tail up, in the limb of the U connected to the recording device; its body was shortened and broadened and filled the tube; its tail was short and thick, with its tip at, or near, the meniscus. As each of the bursts of rapid oscillation set in, the worm suddenly lengthened and narrowed its body. At this stage, there was usually

a drop of the writing point, presumably due to a slight upwards creeping of the worm, though this was not actually seen. Powerful headward wave-movements then began, the worm as a whole remaining in the same position. The waves began at the base of the tail, and resembled vigorous irrigation waves. Each wave drove air along the dorsal surface of the body, nearly to the most anterior gills; at this point, the bubble seemed to slip back past the wave and jerk up to the water surface again. During this phase, the water surface was mostly at the base of the tail. Each wave appears as a small oscillation of the writing point. Finally, the waves became gentler and died out, and the worm resumed its resting position.

The whole performance is clearly identical with the irrigation outbursts seen in the apparatus of Fig. 1. The variability of timing is paralleled by the irrigation records. In particular, there is an attractive resemblance between Fig. 6 and the upper extract in Fig. 9; in both cases, a prolonged outburst of great amplitude is followed by a series of bursts at short intervals. Now the worm of Fig. 9 spent the first $3\frac{1}{2}$ hr. of its time in the apparatus lying very still with its head up the open limb of the U, at about the level of the meniscus. In these circumstances it cannot have got any significant oxygen supply; its first respiratory movements are shown in Fig. 9; so the common features of the two figures may be attributed to previous oxygen shortage.

The first and second phases of the irrigation cycle are usually evident on the air-breathing tracings. The third ('rebound') is not detectable on the records; but as one watches the worm, one sometimes sees a slight, slow wave-creep in the tailward direction as the outburst passes off.

Cyclic aerial respiration of this type was seen or recorded in 13 of the 15 worms used. That it is adequate to support the worm for a considerable length of time was proved by worm no. T 5, which spent 120 hr. in the apparatus, always with the same 15 c.c. of sea water, and was in excellent condition at the end.

We may infer from these results that the worms in the field breathe air intermittently under low-tide conditions, and that they do so by adapting the irrigation cycle. Whether they continue to feed and defaecate when the tide is out will presumably depend on the mechanical properties of the drying sand.

DISCUSSION—THE FUNCTIONAL SIGNIFICANCE OF INTERMITTENCE

Van Dam (1937, 1938) made experiments on the respiration of animals from various phyla, several of which showed intermittent respiratory movements, and he assembled a number of other examples from the literature. The mechanism of intermittence may clearly be very different in different cases. The behaviour of *Arenicola* may profitably be contrasted with that of the larvae of the caddis fly, *Phryganea grandis*. These were studied by van Dam, after he had induced them to assume celluloid cases. They irrigate their cases by means of undulatory movements of the abdomen, and the following citations

from van Dam give the physiological picture: 'Periods of ventilating often very regularly alternated with intervals during which no movements occurred. . . . Crawling and struggling increased the oxygen need of the animal and so caused the intervals to be shortened. . . . That it was really oxygen want which brought about the respiratory movements, was proved in the following way. A tube was attached to one end of the case and a current of water was forced through it. In a current of air-saturated water no ventilation movements occurred (e.g. not for 27 min.), even if the animal moved in its case. However, if water poor in oxygen was used, the intervals were shortened and finally ventilation became uninterrupted. . . . Water containing from about 2 to 29% CO_2 had no marked influence on the respiratory movements.' This is a clear case of reflex response to change in oxygen tension. With *Arenicola*, on the other hand, the position is completely different. Neither in the experiments of van Dam nor in those here described were the pauses abolished or shortened by oxygen lack, and intermittence is seen in worms surrounded on all sides by air-saturated water.

Can one read any functional significance into intermittence? Wolvekamp & Vreede (1941) suggest economy of effort. If the worms are watched, one sees that their whole attitude changes as the irrigation outbursts appear. 'During the pauses the body was contracted and, except the posterior end, pressed everywhere against the tube; the gills were also contracted. The animal usually lay motionless in its tube. Before resuming ventilation the animal elongated its body' (van Dam, 1938). Perhaps this change in posture means an increase in muscle tone and in the pressure of the body fluids, for clearly the latter factor must be high if effective irrigating movements are to be performed. If this be true, it might be economical to pump the necessary amount of sea water in bursts, rather than to do it gently and continuously, for the cost of maintaining an alert posture would be saved during the intervals in the former case. Against this viewpoint, however, it may be pointed out that the worms appear to be more active between the bursts when in sand than they are in glass tubes. This will be shown in another paper. In the absence of measurements of the metabolic cost of the worm's various kinds of activity, the 'economy' argument is not wholly convincing.

The problem can perhaps be more profitably approached from another angle. If the experiment illustrated in Figs. 5 and 6 were carried out on a reflexly irrigating animal, such as a *Phryganea* larva, the result would be as follows. The animal would irrigate more and more violently and continuously—but to no purpose—when the taps were turned to 'no air'; presently it would be exhausted and would cease to show respiratory movements; after this stage has been reached, the turning back of the taps would be of no avail, since the animal must co-operate if it is to get the oxygenated water. *Arenicola*, on the other hand, behaves in a way making for long survival under the conditions of the experiment. When the taps are turned to 'no air', its irrigation

outbursts decrease in intensity; they may perhaps be interpreted as a periodic testing of the conditions; and only when the taps are turned back, and the movements bring aerated water again, is their vigour increased.

It is of course unreasonable to suppose that the worm is adapted to the special conditions of a laboratory apparatus, and one might question whether a similar situation would ever occur in the field. At high tide, the worm has a plentiful supply of oxygenated water at its disposal, and at low tide, if the sand surface dries, it can breathe air. If, however, the burrow were covered with surface water at low tide, then circumstances might arise in which behaviour of the *Phryganea* type would be injurious or even fatal, while behaviour of the *Arenicola* type would save its exhibitor.

The surface water in summer weather is often several degrees hotter than the underlying sand. Linke (1939) studied an *Arenicola* beach near Wilhelms-haven, and found the following temperatures towards the end of a long tidal exposure in July, 1935: water in surface puddles, 26.2°C. ; sand at a depth of 10 cm., 21.3° ; at 30 cm., 19.4°C. I have noticed similar differences, though of less extent, when collecting worms at Thorpe Bay, on the Thames estuary. This is a beach which is exposed for a couple of hours only; nevertheless, it is very noticeable in summer that worms taken away in water collected from the sea travel better than those taken in surface water from the sand flats. When experimenting on dissected worms, or keeping stocks in the laboratory, I regard 20° as about the upper limit for good results. Thamdrup (1935, p. 66) found that the O_2 consumption of *Arenicola* rose from 2° to 10°C. , and from 10° to 20°C. , but fell from 20° to 28°C.

It seems clear that the surface water may become hot enough to be dangerous to the animals, and we may guess that a worm, whose burrow was left at low tide under a pool of hot water, would behave rather like the animal of Fig. 6. It would refrain, for obvious reasons from irrigating its burrow; under the influence of its internal 'clock', it would make occasional testing excursions towards the surface; and, after the returning tide had brought a supply of cooler water, it would begin vigorous irrigation at the next testing excursion. A hard frost, or a heavy rain, might perhaps make the surface water dangerous at low tide, and here again behaviour of the *Arenicola* type would be useful.

The fact that the cycles typically begin with tailwards creeping adapts them to the purpose of testing the surface water, since the worm is thereby brought nearer to the surface. The intensity of the second phase, of headward irrigation, can vary, as we have seen, with the conditions. The third, or 'rebound' phase, may also have its uses; it could expel any harmful water drawn down during testing irrigation, and (since irrigation and antikinetic locomotion are closely related), it might conceivably serve to bring the worm away from the surface if the second phase has been cut out.

These suggestions imply, of course, that the worm can survive long periods of oxygen lack. The animal of Fig. 6 responded promptly to the renewal of the

oxygen supply after 7 hr., during which it can have had little external oxygen except that dissolved in the water in the U-tube, the capillary and the short connecting tubes.¹ No analyses of oxygen tension were made, but the conditions were at any rate stringent enough to induce a marked change in behaviour soon after turning the taps to 'no air' (Fig. 5).

On the question of the possible value of haemoglobin as an oxygen store, the available data are meagre. Estimates of the oxygen consumption of the worms (when shaken in a little sea water in a manometric apparatus) and of the oxygen capacity of the worms' blood were made by Barcroft & Barcroft (1924), who deduced that the oxygen in the blood, at saturation, would be 'enough to suffice the worm for an hour or thereabouts'. Similar measurements and calculations were made by Borden (1931), who concluded that the oxygen in the blood would last 71 min.—a result in good agreement with that of Barcroft & Barcroft, although the figures on which it is based are considerably higher.² Thamdrup (1935) made measurements of the oxygen consumption at various temperatures with the Winkler technique; his figures fall between those of Barcroft & Barcroft and those of Borden.³ Two further points should be borne in mind. The first is that the calculations just cited assume that the worms will continue, in the absence of an external oxygen supply, to consume oxygen at the same rate as when it is abundantly available. This has not been shown to be true, and the behaviour of the worms in Figs. 5 and 6 suggests that, on the contrary, the energy usage is reduced when the oxygen supply falls. The second is that *Arenicola* has recently been found to have haemoglobin in its muscles, besides that in its blood (Fox, 1949). Both of these factors will tend to prolong the period over which the stored oxygen will last. Van Dam (1938) accepts the earlier values (about 1 hr.'s supply) and suggests that the function of the haemoglobin is to supply the worm in the intervals between consecutive irrigation outbursts. According to the hypothesis here put forward, unfavourable surface conditions may force the worm to do with little or no external oxygen during the whole of the low-tide exposure period.

SUMMARY

The worms were housed in glass U-tubes, and were able to get a supply of aerated water from above by making pumping movements. The water movements were recorded kymographically. The experiments generally lasted for 24 hr. or longer.

The worms generally settled down to give outbursts of irrigation separated

¹ Total volume of water about 35 c.c.; the total O₂ content of this would be, at the start, about 0.2 c.c.; the worm weighed 4.8 g.

² The oxygen consumptions, in c.c. O₂/g./hr., are 0.01 (Barcroft & Barcroft) and 0.02–0.04 (Borden). The oxygen capacities of the blood, in c.c. O₂/g. of worm, are 0.008–0.013 (Barcroft & Barcroft) and 0.030–0.049 (Borden).

³ Oxygen consumption, in c.c. O₂/g./hr., 0.0064 at 2°, 0.015 at 10°, 0.034 at 20°, 0.018 at 28°C.

by periods of rest, the alternation continuing with great regularity for many hours at a stretch.

An irrigation outburst consists of three phases: (a) tailward locomotion, (b) headward irrigation and slow headward creeping, (c) tailward irrigation. These three phases always follow each other in that order, but their relative prominence is variable. The second phase is the most conspicuous, whenever a plentiful supply of oxygenated water is available.

The following facts show that the intermittence is spontaneous, i.e. produced solely by conditions internal to the worm:

(i) If worms are pinned down in large vessels of well-aerated and stirred sea water, they often show outbursts of rhythmic activity corresponding in timing to the irrigation cycles.

(ii) Van Dam (1938) found that the pauses between outbursts are neither shortened nor abolished by lowering the oxygen tension in the water.

(iii) If the experimental conditions are so arranged that the worm can circulate the water in its U-tube without thereby getting an oxygen supply, the irrigation cycles continue with their previous timing, but with the vigour of the outbursts greatly reduced. If, after some hours under these conditions, aerated water is again admitted, irrigation is very greatly increased.

Observations on the rhythmic activity of body-wall strips indicate that the pacemaker for the irrigation cycles is in the ventral nerve cord.

If worms are placed in U-tubes partly filled with water, so that circulation is impossible, they creep tailwards to the water surface and draw air down into contact with their gills. Aerial respiration is intermittent, and is brought about by an adaptation of the irrigation cycle.

Intermittence, determined by an internal pacemaker, might have survival value if, at low tide, the burrow was covered by surface water which got too hot, or otherwise dangerous, for the worm.

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THE BEHAVIOUR OF *ARENICOLA MARINA* L. IN SAND, AND THE ROLE OF SPONTANEOUS ACTIVITY CYCLES

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(Text-figs. 1-7)

In the laboratory, the lugworm shows two distinct types of spontaneous activity cycle. The question which the following paper sets out to answer is, have these laboratory results any bearing on the worm's normal life in the field?

The first type of cycle has tentatively been named the feeding cycle. The isolated oesophagus, suspended in sea water or the worm's body fluid, shows outbursts of rhythmic activity alternating with periods of rest. The intact worm, watched in a glass tube, generally shows periodic outbursts of proboscis extrusion and withdrawal, or of gulping and swaying of the head. These cycles, like those of the oesophagus, have an average period of about 7 min. By means of a series of dissected preparations of ascending complexity, one can show that the two rhythms are the same; the 'feeding rhythm' of the whole worm is the oesophageal rhythm, transmitted to the muscles of the proboscis and the anterior body wall (Wells, 1937).

The second type of cycle is of much longer period. The worms, in glass tubes, generally pump water through the tubes in a headward direction in rhythmically recurring bursts. Closer inspection shows that this headward irrigation is the second, and most prominent, phase of a 3-phase outburst; the first is tailwards locomotion, and the third is tailwards irrigation. The outbursts are not, as one might expect, reflexly elicited by oxygen exhaustion or CO₂ accumulation in the tube, but result from the activity of a second pacemaker, probably situated in the ventral nerve cord (van Dam 1937, 1938; Wells, 1949).

Now the intact worms, in all of these experiments, were watched under abnormal conditions. A glass tube differs, mechanically and chemically, from the sand in which the species normally lives; in order that their activities should be visible, the worms were illuminated; and they had mostly been fasting in the laboratory for days or even weeks. One might therefore suspect that the very regular periodicity, which so often characterizes their behaviour, is due to the artificial conditions and would not occur, or would be masked by reflex responses, in the more variable surroundings in the field.

To settle this point, one would have to watch or record the behaviour pattern of the worms in their natural habitat. This would be difficult. I have therefore

done the next best thing, and allowed worms to make burrows in sand in the laboratory, in which their behaviour could be recorded. The results are described below. The main conclusion is that the cycles appear with great regularity, and especially clearly when the worms are making funnels and faecal accumulations like those which signalize their presence on the beach.

THE FORM OF THE BURROW IN THE FIELD

The animal's mode of life has been described elsewhere (Wells, 1945).¹ The details of the burrow vary according to the nature of the beach, but there is

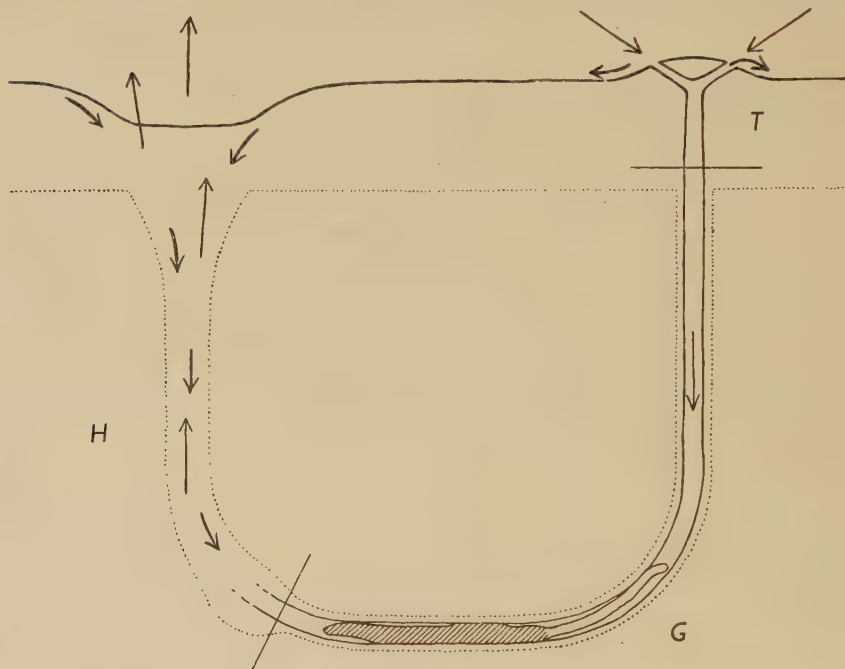


Fig. 1. Generalized diagram of a lugworm burrow, with the worm lying quietly in the gallery. The cross lines are drawn at the boundaries between head shaft (*H*), gallery (*G*) and tail shaft (*T*). The dotted line is the boundary between yellow and black sand. The long, thin arrows show the movement of water, and the short, thick ones that of sand.

a general pattern to which all of the variations conform (Fig. 1). Immediately below the well-known heap of castings, a 'tail shaft' descends vertically for several cm.; this houses the tail at the moment of defaecation. At its lower end,

¹ When I wrote that paper, I was unaware of two important works on the form of the lugworm's burrow. Häntzschel (1938) described burrows in sand. Linke (1939) described burrows in sand and mud, and gave much interesting information about the environment. Both accounts are illustrated by photographs and both stress the fact that the form of the burrow varies with the nature of the bottom.

the tail shaft widens into the 'gallery', a tube in which the worm moves to and fro, but always with its tail towards the tail shaft. The walls of the gallery are firm, due to impregnation with the worm's secretions (Osler, 1826; Häntzschel, 1938; Linke, 1939). The gallery descends more or less vertically, then swings round to become horizontal. Its lower ending communicates with the surface by the 'head shaft', a part of the burrow whose detailed structure varies greatly with the nature of the beach. Typically, the head shaft consists of a column of yellowish sand, without any lumen running through it, and its upper end is marked by a saucer-shaped depression of the surface. The chief forces by which the head shaft is set up and maintained are: (i) feeding from its lower end, causing its substance to slowly descend; (ii) upstreaming of the irrigation water, which helps to keep it soft; and (iii) occasional upward 'working' excursions of the worm.¹ If the conditions are favourable, a worm may live in the same burrow—irrigating, feeding and periodically defaecating—for months on end (Thamdrup, 1935; Linke, 1939).

APPARATUS FOR STUDYING BEHAVIOUR IN THE BURROW

To watch the activities of a worm in sand is impossible. Even if one allows it to burrow between glass plates, so close that there is only just room for the worm, sand makes its way between worm and glass, and one gets only occasional glimpses of parts of the animal. The method used in this work was to record the water currents set up by the worms in their burrows, and to compare the resulting records with those produced by worms in glass tubes (Wells, 1949). The apparatus was as follows.

ABCD (Fig. 2) represents two squares of plate glass, about 38 cm. square. They are held apart by a U-shaped strip of rubber (shaded), which is of square section and about 1 cm. thick. This rubber is well greased with stopcock grease on the sides which meet the glass, and shorter pieces are put beside it at six points; at these places, the whole is held together by *G*-clamps, lightly applied through additional rubber pads external to the glass. Another greased rubber strip, in the centre, divides the upper part of the resulting vivarium into two.

When assembled, the vivarium is held upright in a wooden stand (not shown) and filled. The lower part contains, to a depth of about 20 cm., mud dug from the deeper layers of the beach (drawn black). On top of this is about 6 cm. of yellow surface sand (dotted), and 6 cm. of sea water. Aeration is through jet *E*. Finally a large, recently collected worm is added. The worm goes down into the mud at once, and one usually sees nothing more for a day or so; but the dimensions are such that it ultimately sets up a burrow with the funnel on one

¹ Chapman & Newell (1947, 1948) believe that the thixotropy of muddy sand plays an essential part in the processes by which the worm enters the sand and sets up a burrow, but the writer is unable to see the necessity for this (Wells, 1948).

side of the centre partition and the faecal pile on the other, as shown in the drawing.

Water currents are produced by the worm in various ways—by irrigation, or by creeping along the tube—and will clearly tend to displace the levels of the water in the two top compartments. The muddy sand is practically impermeable to water. The compartments are connected by capillary siphon *F*,

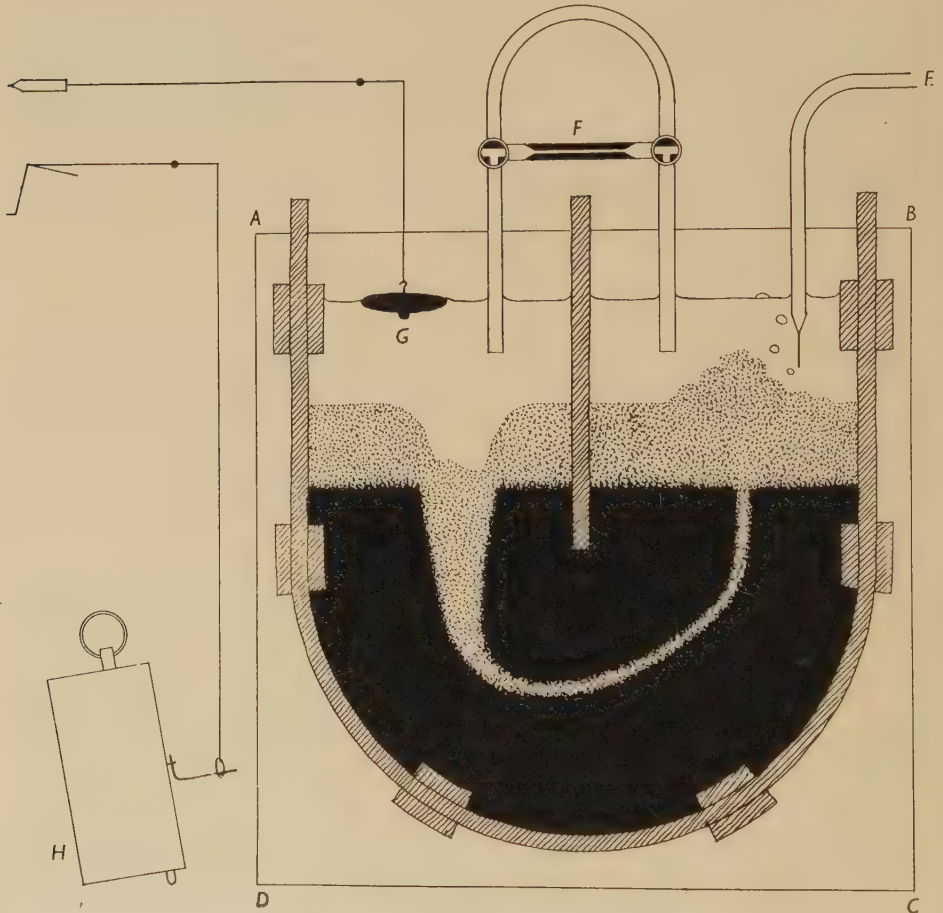


Fig. 2. Apparatus for recording the behaviour of the worm in the burrow (see text).

provided with a by-pass of wide bore to facilitate the daily routine, described below. The capillary prevents excessive piling up of water on either side, but offers enough resistance to allow the fluctuations in level to be recorded. This is done by means of float *G*, made of paraffin wax moulded on silver wire, and connected to a light isotonic lever writing on smoked paper.

The following values were found satisfactory: capillary bore about 1.5 mm.; lever magnification about 12; paper moves at about 25 mm./hr. The time trace was made by clock *H*, connected to a lever with a frontal writing point and tracing 1 cycle per hr.; it has been omitted from the illustrations to save space.

Once a day, the following routine was carried out. The smoked paper was changed, the wide by-pass siphon was opened, the sea water was topped up with distilled water to a gauge mark to compensate for evaporation; the faeces were removed and fresh sand was added to the funnel. Except for this daily operation, which took about 5 min., recording was continuous and the apparatus ran itself.

Altogether, six worms were studied, for periods ranging from 5 to 21 days; they yielded an aggregate of 72 recorded 'worm-days'. None of these worms died during the experiments and five of them were still in good condition in the sand when their records were stopped. The sixth ended its experiment by coming out on the surface of the sand on the 11th day and refusing to go down again (though apparently in good condition) for 36 hr.; this was probably due to some kind of organic decomposition in the sand. I have noticed, on other occasions, that the worms tend to leave very foul sand, and when the vivarium of this particular individual was dismantled it was unusually evil-smelling.

THE FORM OF THE BURROW IN THE APPARATUS

The configuration of the burrows in the apparatus (as shown by a yellow stain on the black sand) resembled that found in the field. The worms fed from conical head shafts (whose upper surfaces subsided rather more rapidly than usual owing to the small sectional area of the apparatus) and piled up heaps of faecal cylinders. They appeared, however, to be rather more restless than worms kept under less cramped conditions. The head shafts often shifted a little in position from day to day, and the worms sometimes reversed their burrows, converting the old tail shaft into a head shaft, and vice versa. Both of these changes are occasionally seen in larger vivaria (and they undoubtedly occur in the field), but they were rather more frequent in the apparatus here described.

THE DEFAECATION CYCLE

Whenever the worms were feeding regularly from the head shaft, and piling up their faeces in the other compartment of the apparatus, the pattern shown in Fig. 3 was traced on the record. The obvious feature is a series of prominent diphasic excursions with a sharp, short peak followed by a broader one in the opposite direction. They occur about once every 40 min.

Now this record can very readily be interpreted by means of the experiments with worms in glass tubes. The cycles traced in Fig. 5 of my previous paper

(Wells, 1949) are evidently identical with those now under consideration.¹ We may safely conclude that the movements responsible for the tracings are the same in both cases. The sharp first peak is due to a tailward excursion of the worm, and the broad second peak is due to vigorous headward irrigation accompanied by gentle headward creeping. The third 'rebound' phase, which was sometimes very conspicuous in glass tubes, is seldom visible on the records got from actively feeding worms in sand.

If one watches the experiments with worms in sand, one sees that a faecal cylinder is suddenly shot out of the burrow at (or a moment before) the apex of each of the sharp peaks. In other words, the tailward excursion, which

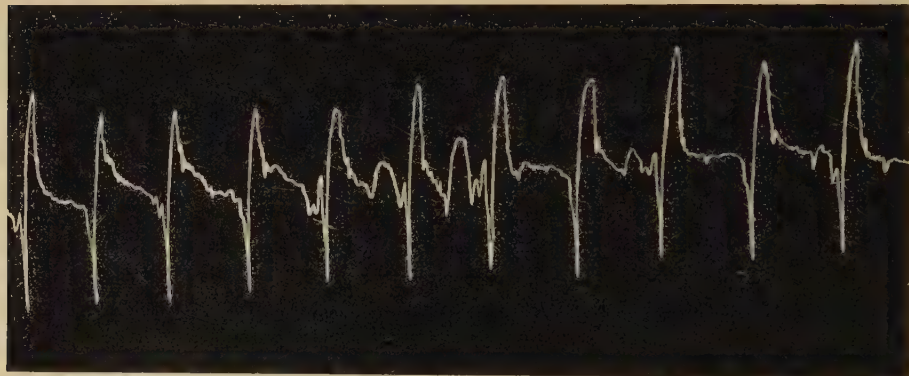


Fig. 3. Record (7 hr. long) traced by an actively feeding worm, with its tail towards the float. The worm defaecates at the tip of each of the prominent downward peaks. Read from left to right. (Worm 'Violetta'.)

begins the whole outburst, has carried the worm to the surface of the sand, and serves as a defaecatory excursion. The worm presumably creeps back to the point where it feeds, at the lower end of the head shaft, during the phase of headward irrigation.

One might have thought that the tailward excursion which brings the worm into position for defaecation is a reflex response to a full rectum, but this does not seem to be the case. Exactly similar excursions were often seen in glass tubes, in worms which had been fasting for days and whose tails were consequently empty.² We must therefore conclude that the tailward trip is simply an expression of one of the phases of the triphasic cycle, which is very beautifully suited to the worm's normal way of life.

¹ The worm in Fig. 3 of the present paper has its tail to the float, while that in Fig. 5 of the previous one is the other way round; so the patterns are traced the opposite way up.

² The worms occasionally produced faeces in the U-tubes but only if studied within 24 hr. of collection, and unfortunately never while they were being watched. The worm O 48 (in Fig. 5 of the previous paper) was collected on 11 January 1949, kept in a glass tank of clean sea water, and then put in the apparatus on 14 January 1949; its behaviour was recorded for 48 hr., during which two exposures to 'no air' were tried. The record shown in the illustration was taken in the evening of 15 January 1949.

ALTERNATIVE BEHAVIOUR PATTERNS

The pattern just described invariably accompanied feeding and defaecation. Having once set in, it was generally written on the drum with great regularity for many hours at a stretch, while the faeces steadily piled up and the funnel subsided. During the rest of the time, records were obtained which can be classified into three groups.

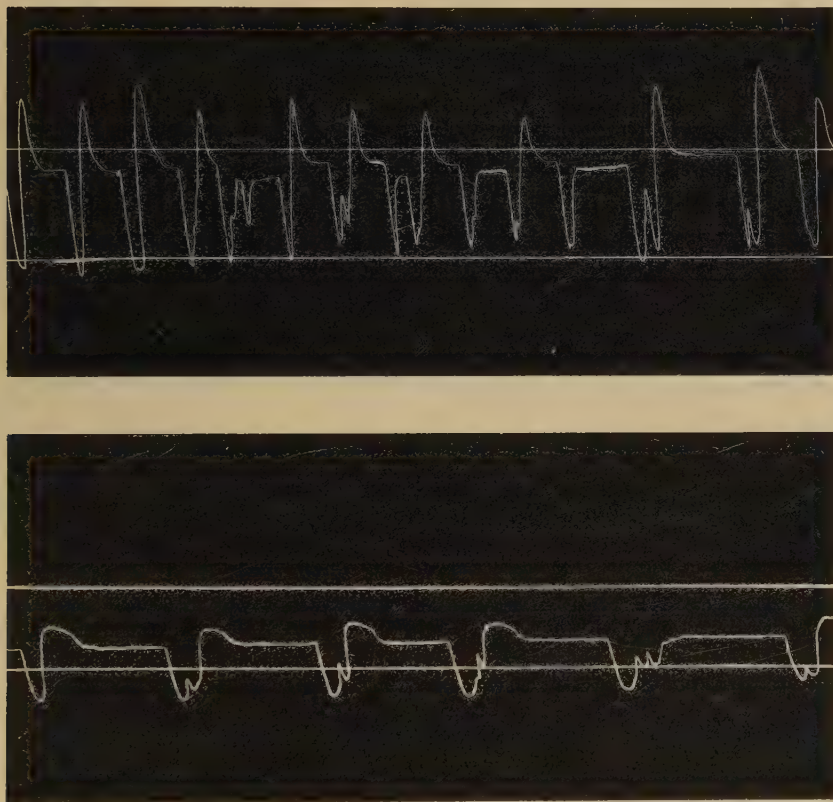


Fig. 4. Two records (each $4\frac{1}{2}$ hr. long) traced by a worm which was not actively feeding and defaecating. The extracts were given on two different days. In both cases the worm's head is towards the float. The horizontal lines give the resting water levels at the beginning and end of the day. The difference is due to evaporation, which also causes the gradual upward trend of the other figures. (Worm 'Fasolt'.)

(i) *Irrigation cycles without a pronounced tailward excursion.* In sand, as in glass U-tubes, the three phases of the typical cycle can vary greatly in their relative prominence. The two records of Fig 4 were taken from the same worm, on different days, and in both cases its head was towards the float. They represent irrigation cycles in which the first phase is barely perceptible on the

tracing, while the second and usually the third are well marked (compare Wells, 1949, second part of Fig. 6). Now and again, one sees an outburst in which the third, 'rebound', phase is dropped out, and the same thing can be seen in the records got from glass tubes. With this curious exception, it may be stressed that the outbursts in any single series have an extremely constant form. The various types are modifications of an underlying triphasic pattern; having made up its mind, so to speak, which type to register, the worm sticks to that type very steadily for hour after hour. On another day, of course, it may choose another.

(ii) *Periods of apparently complete quiescence.* The lever sometimes traces a horizontal line, with barely perceptible oscillations if any, for many hours on end. One would like to know what the worm is doing, and especially how it gets oxygen, at such times. One knows only that it is inside the sand, whose untroubled surface gives no clue to what goes on below. Quiescence may continue for 24 hr. or even longer, after which vigorous activity begins again and the regular rhythmic patterns reappear.

(iii) *Periods of unexplained activity.* The lever shows excursions, often of very great amplitude, but the tracings are confused and have successfully defied all attempts at interpretation. This may continue for many hours.

Taking together all of the six worms which were studied in sand, their total time was divided between the various patterns as follows: defaecation cycles, 45%; other irrigation cycles, 5%; quiescent spells, 15%; periods of unexplained activity, 35%. It will be seen that only about half of the records obtained have been satisfactorily interpreted.

These results can be extrapolated, with due reservation, to the behaviour of the worms in the field. It may, I think, be fairly safely assumed, that every saucer and pile of faeces on the beach is the outcome of a cyclic behaviour pattern like that seen in Fig. 3. Mrs D. M. Kermack, who is studying the feeding and digestion of *Arenicola*, informs me that under favourable conditions the worms in the field defaecate about once every 45 min. This agrees well with the timing of the peaks in my records. My results also suggest that, at any moment, a considerable proportion of the worms is giving no surface signs at all—but the relative magnitude of the 'hidden population' will presumably vary with conditions. Newell (1948) assessed the density of lugworm populations by digging up areas of 1 sq.yd., and wrote 'This rather tedious method of sampling was found to be essential, since counting the number of casts per square yard is a most unreliable index of the number of worms, varying as it does with, among other conditions, the state of the tide'. There was, of course, no tide in my experiments. The time spent in active feeding and defaecation varied in different individuals from 32.5 to 68%; so it may be that the conditions determining activity are not entirely environmental. I have already described great differences in feeding activity between worms kept individually in aquaria (Wells, 1945).

THE FEEDING CYCLE

As stated in the opening paragraphs, two distinct types of behaviour cycle are shown by lugworms in glass tubes. There is the irrigation-defaecation cycle already dealt with, and there is a cycle of anterior end activity, of period averaging about 7 min., which has been tentatively named a feeding cycle (Wells, 1937). Now the records got from worms in sand often show a considerable amount of 'background' activity between the irrigation-defaecation outbursts, and sometimes this has an obviously cyclic pattern, with a period of the same order as that of the feeding cycle. The extract of Fig. 5, for example,

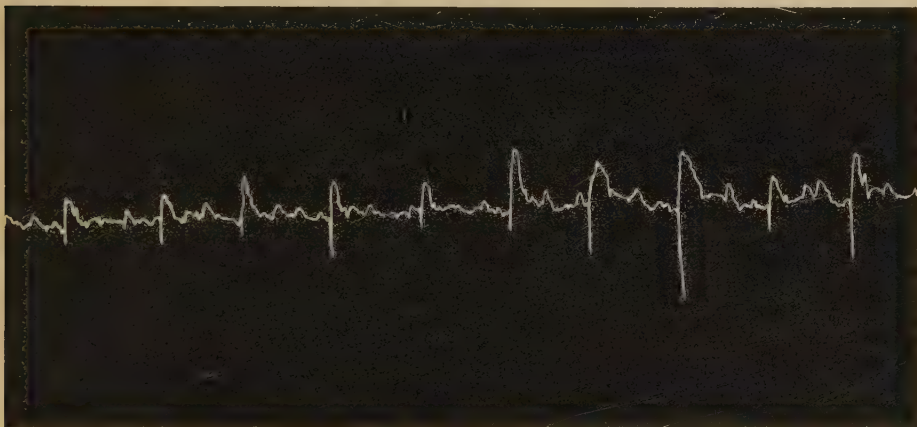


Fig. 5. Record (6 hr. long) traced by an actively feeding and defaecating worm, with its tail towards the float. The record shows a short-period cycle imposed on the main one. (Worm 'Sieglinde'.)

shows defaecatory excursions at intervals of about 35 min., and minor oscillations with a period of about 7–8 min. These may well be due to the oesophageal pacemaker, but it remains to be shown how the feeding outbursts could write themselves on the drum, with the apparatus of Fig. 1.

Just (1924) pointed out that there is a functional differentiation between the nineteen chaetigerous segments in the lugworm's body. The first three participate in the movements of the head and especially in proboscis activity, while the wave movements, which run along the body in irrigation or creeping, are the concern of the remaining sixteen. I showed in an earlier work that the excitations responsible for the feeding outbursts spread from the oesophagus to the body-wall muscles of the more anterior segments, which play a direct part in proboscis activity (Wells, 1937). The experiments now to be described were made to find out whether any influence of the oesophageal rhythm could be traced in the wave-carrying segments farther back.

The worm was pinned on a cork sheet under sea water, ventral side down

(Fig. 6). The first few segments were laid open and the extrovert was dissected as described in my earlier paper (Wells, 1937). The oesophagus was cut across and its oral end was connected to a light isotonic lever. The movements of this lever are mainly due to the proboscis muscles acting under the influence of the oesophageal pacemaker, though the muscles of the surrounding body wall also contribute to some extent. One or two of the branchiate segments were

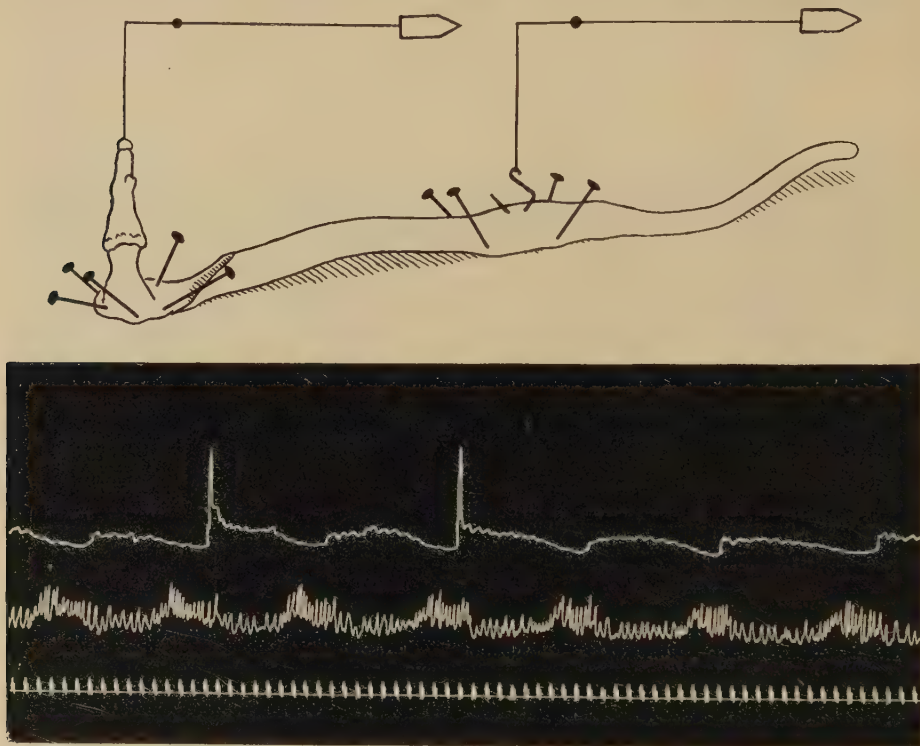


Fig. 6. Method for studying the influence of the oesophageal outbursts on the branchiate segments (above), and a record obtained in this way (below). The lower line of the tracing was made by the extrovert, and the upper by the body wall. Read from left to right; time scale in minutes. (Worm E/I 8.)

immobilized by pins inserted latero-ventrally (but avoiding the nerve cord), and a hook inserted mid-dorsally in the same region was connected to a second lever.

The results were rather capricious. In most of the worms so treated, an inhibitory influence of the oesophageal outbursts on the branchiate region could be detected. Fig. 6 gives a typical tracing; the lower line (from the oesophagus) shows the outbursts of extrovert activity, following each other in this case at intervals of 12 min., and the upper trace (from the body wall) shows very clearly how the body wall relaxes and suspends its slight spontaneous movements at each of the oesophageal outbursts. In two of the cycles, there

is an upstroke of the body-wall lever as the oesophageal outburst passes off; and this effect was seen from time to time in several of the worms.

Fig. 7 shows an experiment in which the body wall was unusually active; one can see very clearly that the inhibitory effect of the extrovert is on the amplitude, not the frequency, of contraction in the body wall.

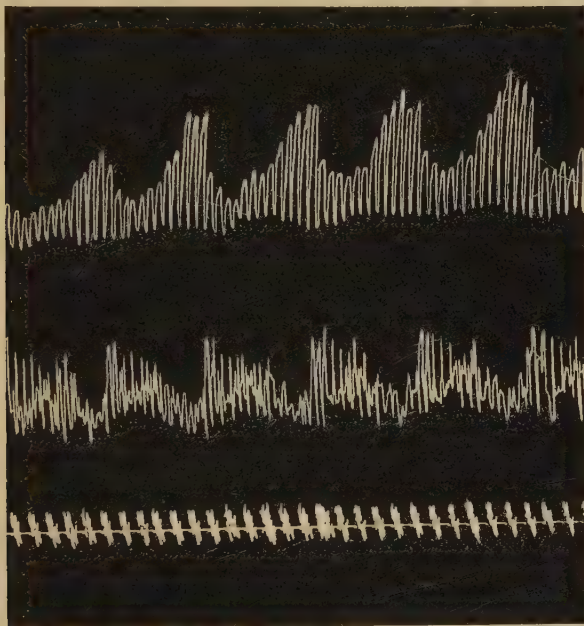


Fig. 7. Record, got by the method of Fig. 5, showing decrease in amplitude of the body-wall contractions (above) at each outburst of the extrovert (below). Time scale in minutes. (Worm E/I 4.)

These results show that the oesophageal pacemaker influences the hinder segments, though the acts of proboscis extrusion and withdrawal concern only the more anterior ones (and can be carried out by these segments after the rest of the worm has been removed). By doing so, it could influence the water-movement tracings, since the latter are produced by the activity of the wave-carrying segments. I have not as yet been able to devise means of pursuing this question into further detail. As far as they go, the results are at least not inconsistent with the view that the oesophageal pacemaker determines periodic feeding when the worm is in sand.

DISCUSSION

To a large extent, the various activities of which a lugworm's behaviour cycles are made up are 'whole worm' activities, i.e. it cannot do more than one of them at any given moment. Vigorous tailward locomotion and vigorous head-

ward irrigation both depend on headward waves, but the attitude of the worm is different in the two cases. The facts described in the last section suggest that feeding, too, concerns more than the first few segments. Since the worm must do all of these things, and cannot do them all at once, its life must have a pattern; and because the worm's environment, once it has established itself in a favourably situated burrow, is exceedingly uniform, the pattern will result more from its own internal processes than from the impact of external events. A predator can only feed if it encounters suitable prey; *Arenicola* can eat whenever it feels so disposed, at least during the period of high tide. It already follows from these considerations, that the pattern of a lugworm's life will be pretty regularly cyclic, as long as it is comfortably settled in a burrow.

Such an integrated pattern could be achieved by means of a hierarchy of reflexes with appropriate responses to the worm's various needs—to an empty gullet, to a full rectum, and to oxygen lack or CO₂ excess. But all the evidence suggests that in *Arenicola* the organization is based quite differently, on spontaneously active 'clocks' in its oesophagus and nerve cord. This does not mean that the rhythms cannot be modified: we have seen that they can; but it means that the various activities can take place under conditions in which the corresponding needs can neither arise nor be satisfied. Defaecatory excursions may occur when the rectum is empty (Wells, 1949, fig. 5). Intermittent irrigation may occur when the worm is surrounded by well-aerated water (Wells, 1949, fig. 4). If the interpretation of the proboscis outbursts as feeding cycles is sound, then the feeding pattern occurs when the worm has been reduced to a shred of the oesophagus, all the rest of the body having been removed (Wells, 1937).

With regard to the adaptive significance of this type of organization, it has already been pointed out that under conditions which may arise from time to time in the field, intermittent irrigation cycles based on a 'clock' would have a greater survival value than those based on reflex responses to respiratory needs (Wells, 1949). The function of the presumed feeding cycle is not clear; perhaps it will come to light when the physiology of digestion in *Arenicola* is better understood.

With regard to the intimate mechanism of the cycles, it may be pointed out that both the feeding cycle and the irrigation-defaecation cycle consist of the periodic evocation—or perhaps the periodic suppression—of processes which are in themselves rhythmic. Proboscis activity, irrigation, creeping—in each of these there is a fairly rapid alternation of phases, as in a beating heart or a swimming dogfish. Such an alternation could be due to a spontaneous pacemaker, as in the heart, or to a reflex system in which each phase is the stimulus for the next, as in the dogfish (Lissmann, 1946). But the activity cycles of *Arenicola* involve bursts of rhythm separated by periods of rest; the latter, in the case of the irrigation cycles, may be of half an hour's duration; one can hardly suppose that a reflex chain is the determining factor. The same

argument holds for the oesophageal pacemaker, particularly when slowed up by magnesium excess (Wells & Ledingham, 1940). Here again, the outbursts may succeed each other very regularly, though separated by half an hour or so of complete quiescence. There must be a 'clock' mechanism, presumably of the nature of a relaxation oscillator. Occasionally, under abnormal conditions, an isolated vertebrate or crustacean heart shows grouped beats which greatly resemble the intermittent pattern of an isolated *Arenicola* extrovert (Wells, 1937); it may be that the behaviour of the lugworm's pacemakers represents a normalization of this condition.

SUMMARY

Worms were allowed to burrow in sand in the laboratory. The general form of their burrows resembled that found in the field. Their behaviour was studied by continuously recording the water movements through the burrows for periods up to 3 weeks.

Whenever the worms were feeding from a gradually subsiding cone and piling up castings, as they do in the field, a characteristic cyclical pattern was traced. This was marked by conspicuous diphasic excursions at intervals of about 40 min. Defaecation occurs at the summit of the first phase. By comparison with records got from worms in glass tubes (Wells, 1949), it is inferred that the first phase consists of tailward locomotion to the sand surface, and the second to headward irrigation accompanied by gentle creeping back to the feeding point. The whole cycle is identical with the intermittent irrigation cycle shown in glass tubes.

In the intervals between the defaecation-irrigation outbursts, the tracing often shows a periodicity of smaller amplitude and period. This is probably due to intermittent feeding, under the influence of the oesophageal pacemaker (Wells, 1937). Experiments with dissected worms showed that an inhibitory influence of the oesophageal pacemaker can be detected in the segments responsible for creeping and irrigation.

The behaviour described above occupies about 45% of the records (covering altogether 72 'worm-days'). Once having begun, it usually continues very regularly for many hours. For the rest of the time, other patterns were seen, which are described in the text.

The application of these results to the worm's life in the field, and the dependance of feeding, irrigation and defaecation on spontaneously rhythmic pacemakers, are discussed.

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ON THE HYDROID OF *EUTIMA GRACILIS* (FORBES AND GOODSIR)

By F. S. Russell, F.R.S.

Director of the Plymouth Laboratory

(Text-fig. 1)

In July 1938 I succeeded in rearing the hydroid of *Eutima gracilis* (Forbes and Goodsir) (also known as *Saphenia gracilis*) from adult medusae which liberated their eggs and sperm in finger-bowls of sea water. These hydroids were only in the primary polyp stage, and I withheld publication hoping to repeat the work

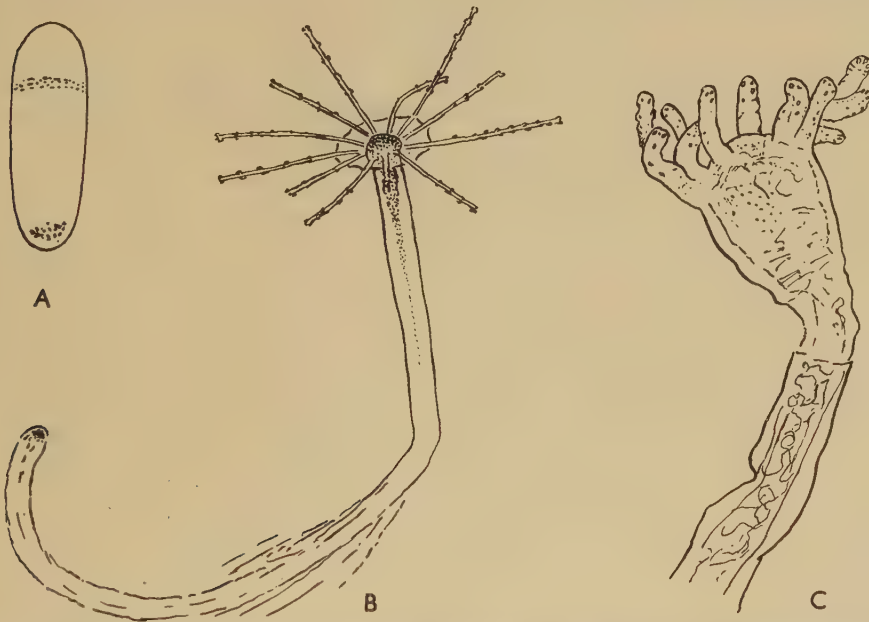


Fig. 1. *Eutima gracilis* (Forbes and Goodsir), Plymouth, 22-23 July, 1938. A, planula, showing position of blue pigment granules; B, primary polyp, showing blue pigment granules at end of stolon and on hydranth at base of tentacles (alive); C, primary polyp, fully contracted (preserved).

later and perhaps rear the hydroid to a more advanced stage. As it is unlikely that I may now have the opportunity of doing this it seems worth while to publish a short account with figures of the polyp.

I have been unable to find any notes I may have made at the time, but the original drawings are available. The planula (Fig. 1A), which is otherwise

colourless, is characterized by a girdle of blue pigment granules near its anterior end and a mass of similar granules situated posteriorly. Fig. 1B shows the primary polyp. The hydranth has a single whorl of twelve filiform tentacles whose bases are united by a membranous web. The hydrocaulus is simple and there is no hydrotheca; the hydranth is thus naked and unable to retract within the perisarc walls which at this stage are very delicate and transparent (see Fig. 1C). At the original point of attachment of the stolon to the substratum the blue pigment granules are still present, and the hydranth itself has blue pigment just below the whorl of tentacles. Unfortunately, I am unable to give measurements.

In its two chief characteristics, namely the presence of a membranous web uniting the bases of the tentacles and the absence of a hydrotheca, this hydroid resembles *Campanopsis* which was described by Claus (1881) as the hydroid of *Octorchis gegenbauri* Haeckel.

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A NOTE ON THE THEORY OF A DWARF RACE OF LOBSTERS ON THE NORFOLK COAST

By Michael Graham

Fisheries Laboratory, Lowestoft

(Text-fig. 1)

At the Annual Conference of Sea Fisheries Committees held in 1947, some members expressed the view that the lobsters being fished at Sheringham belonged to a dwarf race, distinct from the lobsters found at other ports. Such a view, acceptable as it might be to those who have always thought of lobster populations as local, presented certain difficulties to those familiar with Meek's conception of lobsters migrating long distances. Meek (1925) refers to his theory, but has not described evidence to substantiate it.

In this situation, the theory of a dwarf race seemed worth inquiry, and, fortunately, data are available.

The Interdepartmental Committee on Crabs and Lobsters (see its Report on lobsters issued in 1936) instituted investigations of the sizes of the lobsters in various districts in 1938-39, noting separately the sizes of mature females. It was evident that these data would provide the crucial test of the theory of dwarfness, namely an estimate of the size at first maturity in various districts, including that of the supposed dwarfs at Sheringham. English data obtained from these investigations have now been examined.

The data were collected at twelve stations on the English coast. At each station, one fisherman was selected to supply information of the length, sex, and condition of all lobsters in his catches. A copy of the instructions issued to the fishermen, and of the details they were asked to supply, is given in the Appendix (p. 487). (Measuring boards were supplied by the Fisheries Department.) At the same time, Collectors of Fishery Statistics were obtaining statistics of the total landings of shellfish, number of boats used, etc., at the same stations. All English records were returned to the Fisheries Department in London.

These records have now been summarized, port by port, for the period of the investigations—early summer 1938 to autumn 1939—to give distribution by length and sex of marketable and non-marketable lobsters.

Table I shows that, undoubtedly, smaller lobsters were being caught at Sheringham, where, for example, cocks and non-berried hens of less than 8 in. represent 30% of the catch, a higher figure than at any other port. This was doubtless the basis for the belief in a dwarf race of lobsters in this locality, and were this the only statistical guide available, the theory of a dwarf race would not be unacceptable. However, the size-distribution of the mature females

gives the correct solution on this point. In Table II and Fig. 1, which include only mature female lobsters, the figures give the number of berried hens that were taken in each 1 in. group, and show which was the most popular length-group at each port.

It will be observed, in Fig. 1, that at Sheringham, as at all other stations, few berried hens are found of less than 10 in. Furthermore, at six of the ports, including Sheringham, the 10-11 in. group is the largest represented and it shows up conspicuously at still another. The berried hens at Sheringham, then, do not show any marked difference in size from those at other ports. Since these hens are of normal size, it is most unlikely that the lobsters caught off Norfolk belong to a dwarf race.

It may be noted in passing that the same observations make it also unlikely, though not impossible, that the small size is due to stunted growth through local conditions.

The smaller size at Sheringham is most simply expressed as consisting of a higher proportion of young lobsters. This is shown by the following figures, which give the percentage of berried hens in the total catch, extracted from Table I.

North Sea		English Channel		Irish Sea	
	%		%		%
Sheringham	2.8	Eastbourne	2.6	Port Erin	7.9
Whitby	4.6	Beer	19.4	Port Isaac	16.0
Newbiggin	6.5	Looe	2.3		
Beadnell	16.4	Polperro	8.0		
Seahouses	11.4	Scilly Isles	14.4		

It will be observed that only 2.8% of the lobster population caught at Sheringham consisted of berried hens. There are some other interesting points about these figures. The ports are arranged geographically, and the percentage rises from south to north in the North Sea. In the Channel and Irish Sea, there are also some indications of an order in the figures, but with discrepancies, such as the surprising difference between Polperro and Looe, and the high figure at Beer.

From the nature of the data, it is doubtful if much weight can be given at present to these and other points of interest. Only local investigations, properly designed, could give satisfactory information. Points for such investigations are: the apparent absence of any small lobsters at the Scilly Isles; the high percentage of large lobsters shown at Polperro and Port Isaac, in spite of less protection than at some other ports; the high proportion of mature lobsters shown at Beer; and the apparent evidence of difference in the populations fished from the adjoining ports of Polperro and Looe.

The small proportion of fully grown lobsters at Sheringham might be susceptible to either of the following explanations: (i) the stocks at Sheringham may be more severely fished, or (ii) the other North Sea ports, being upstream,

TABLE II. LENGTH OF BERRIED LOBSTERS
(THE NUMBER CAUGHT, AND PERCENTAGE, IS SHOWN FOR EACH 1 IN. GROUP)

Station	No. %	Length (in.)												Total				
		7-	8-	9-	10-	11-	12-	13-	14-	15-	16-	17-	18-					
Seahouses	No.	—	—	15	157	60	215	68	53	40	13	6	1	628	100.0	777*	415	100.0
	%	—	—	2.4	25.0	9.5	34.2	10.8	8.4	6.4	2.1	1.0	0.2	100.0				
Beadnell	No.	—	—	2	33	102	168	173	175	73	23	2	—	777*	100.0	415	100.0	254
	%	—	—	0.3	4.4	13.6	22.4	23.0	23.3	9.7	3.0	0.3	—	100.0				
Newbiggin	No.	1	7	14	64	91	126	81	25	6	—	—	—	415	100.0	299†	100.0	190
	%	0.2	1.7	3.4	15.4	21.9	30.4	19.6	6.0	1.4	—	—	—	100.0				
Whitby	No.	—	—	17	95	70	63	6	2	1	—	—	—	254	100.0	299†	100.0	190
	%	—	—	6.7	37.4	27.5	24.8	2.4	0.8	0.4	—	—	—	100.0				
Sheringham	No.	—	1	37	148	74	32	5	—	—	—	—	—	299†	100.0	556	106	100.0
	%	—	0.3	12.5	49.8	24.9	10.8	1.7	—	—	—	—	—	100.0				
Eastbourne	No.	—	—	15	81	57	21	12	3	1	—	—	—	190	100.0	106	100.0	193
	%	—	—	7.9	42.6	30.0	11.1	6.3	1.6	0.5	—	—	—	100.0				
Beer	No.	—	—	67	237	189	61	2	—	—	—	—	—	556	100.0	177	100.0	539
	%	—	—	12.0	42.6	34.0	11.0	0.4	—	—	—	—	—	100.0				
Looe	No.	—	—	13	57	25	10	1	—	—	—	—	—	106	100.0	177	100.0	539
	%	—	—	12.3	53.8	23.6	9.4	0.9	—	—	—	—	—	100.0				
Polperro	No.	—	—	8	46	64	29	20	20	6	—	—	—	193	100.0	177	100.0	539
	%	—	—	4.1	23.8	33.2	15.0	10.4	10.4	3.1	—	—	—	100.0				
Scilly Isles	No.	—	—	—	8	107	50	8	2	2	—	—	—	177	100.0	258	100.0	100.0
	%	—	—	—	4.5	60.5	28.3	4.5	1.1	1.1	—	—	—	100.0				
Port Isaac	No.	1	—	19	148	280	70	19	2	—	—	—	—	539	100.0	258	100.0	100.0
	%	0.2	—	3.5	27.5	51.9	13.0	3.5	0.4	—	—	—	—	100.0				
Port Erin	No.	—	3	45	106	61	28	9	6	—	—	—	—	258	100.0	258	100.0	100.0
	%	—	1.2	17.4	41.1	23.6	10.9	3.5	2.3	—	—	—	—	100.0				

* Includes 26- size not stated.

† Includes 2- size not stated.

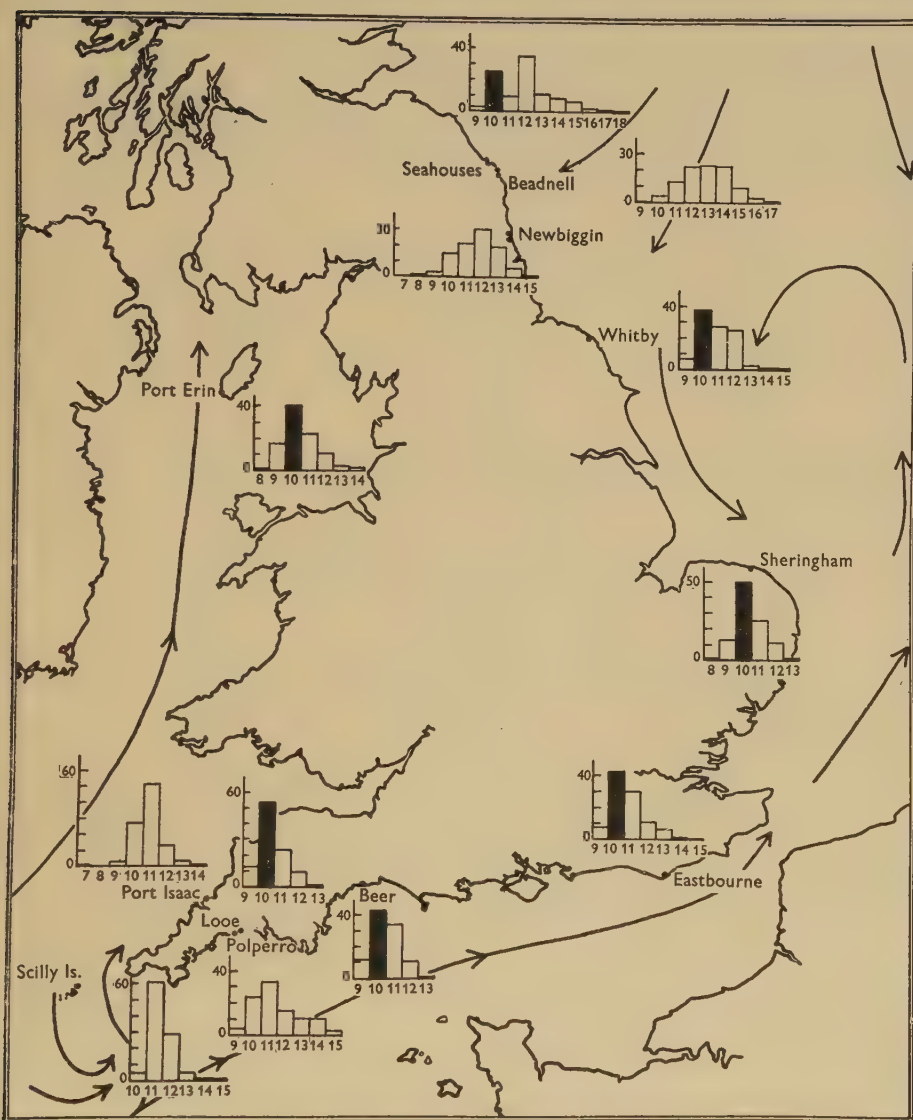


Fig. 1. Lengths of mature female lobsters. The percentage at each length, by inches, reached or passed, of one fisherman's catch of berried hens in 1938 and 1939 is shown for each of twelve ports. At seven of the ports the length group of 10-11 in. shows up conspicuously. The general current system is shown by arrows.

might receive contranant mature lobsters from the Sheringham district, which is downstream.

There is evidence against the first explanation, because a more severely fished stock would be expected to show a lower absolute density of lobsters. This is not so for the lower length-groups. The density at Sheringham of 8 in. lobsters is actually higher than at the other ports. The following figures show the density, based on the index of catch per pot hour.

CATCH PER 10,000 POT HOURS OF 8 IN. LOBSTERS
(COCKS, NON-BERRIED HENS, AND SOFT OR UNDERSIZED)

North Sea		English Channel		Irish Sea	
Sheringham	40	Eastbourne	69	Port Erin	37
Whitby	2	Beer	6	Port Isaac	0
Newbiggin	2	Looe	18		
Beadnell	3	Polperro	2		
Seahouses	6	Scilly Isles	—		

There are several complications to this index, but its main showing can hardly be gainsaid: that at Sheringham 8 in. lobsters are remarkably abundant. Corresponding figures for 9 in. lobsters are as follows:

CATCH PER 10,000 POT HOURS OF 9 IN. LOBSTERS
(COCKS, NON-BERRIED HENS, AND SOFT OR UNDERSIZED)

North Sea		English Channel		Irish Sea	
Sheringham	21	Eastbourne	124	Port Erin	49
Whitby	26	Beer	15	Port Isaac	4
Newbiggin	18	Looe	20		
Beadnell	9	Polperro	8		
Seahouses	19	Scilly Isles	0		

These show no particularly low density at Sheringham.

It is evident that the theory of more severe fishing receives no support from these data. We may again point out that poor nurture would not explain this great abundance, which suggests, if anything, the opposite.

The second explanation, on Meek's theory, satisfies the data much better: namely that the abundance of small lobsters at Sheringham is due to their having drifted there as fry; the rarity of mature lobsters to their having migrated upstream. Meek's theory seems a good fit to these data, but the order of confidence is not as high as if the conclusions were based on a sufficient marking experiment.

Another factor that may contribute to the proportion of berried hens at various ports, and to the sizes of lobsters generally, is the fact that at the Northumberland ports the return of berried hens to the sea has been encouraged for longer than in other districts, perhaps causing more, and larger, hens to be found there.

I wish to acknowledge the assistance of Administrative and Statistical Officers of the Fisheries Department, in the preparation of this paper.

SUMMARY

The evidence points strongly to the effect that Sheringham fishes the same race of lobsters as ports farther north. The most likely explanation of the smaller average size of the lobsters at Sheringham, which is shown to be due to abundance of small and-rarity of large, is that it is in some way natural, and not due to fishing. A neat theory to fit the facts is Meek's, based on the position of Sheringham downstream in the main current system.

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APPENDIX

The following instructions were issued on the front of the log book in which fisherman were to enter details of their catches:

1. Measure the whole catch.
2. Each lobster is to be measured from the tip of the beak to the end of the tail-plate.
3. All measurements are to be made in quarter inches and recorded by the last quarter inch reached or covered: thus, if the division at $10\frac{1}{4}$ inches is covered but that at $10\frac{1}{2}$ inches is not reached, the measurement is to be recorded as $10\frac{1}{4}$.
4. Each length is to be recorded in a separate square.
5. The total number of each sort of lobster taken must be entered on the back of the form, including those rejected.
6. The forms, when completed, should be removed from the pads and handed to the Collector of Fishery Statistics on Monday of each week.

The details requested (Form no. **B 438/F.G.**) were as follows:

On the front of the form were columns for entering lengths under the headings of:

Landed: Cocks; hens, not berried; hens, berried. Returned to the sea: berried hens; undersized or soft.

On the back of the form entries had to be made against:

Date... Ground... Depth... Number of pots lifted... Number of hours since pots were set... How many undersized returned to the sea?... How many soft returned to the sea?... How many berried hens returned to the sea?... How many berried hens landed?... How many non-berried hens landed?... How many cocks landed?... Other shellfish taken in pots and landed: crabs... crawfish....

THE OCCURRENCE OF UNUSUAL SPECIES OF CHAETOGNATHA IN SCOTTISH PLANKTON COLLECTIONS

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There are six species of Chaetognatha that are usually taken in Scottish plankton samples from the appropriate localities. These are

Sagitta setosa J. Müller, from lower salinity water such as that found in the southern and central North Sea and the Irish Sea.

S. elegans elegans Verrill, from mixed oceanic and coastal water.

S. serratodentata Krohn, from surface and subsurface warm oceanic water of fairly high salinity.

S. maxima (Conant), from cold deep water.

Eukrohnia hamata (Möbius), from cold deep water.

Sagitta lyra Krohn, from warm deep water.

All are valuable indicator species (Meek, 1928; Russell, 1935, 1939; Fraser, 1937, 1939). Of these, the first five have occurred in somewhat varying numbers and distribution according to hydrographic conditions every year since at least 1935, except possibly during the period 1940-45 when no investigations were made. *S. lyra* has been taken in most of these years, but was not found in 1935, 1936 or 1937. It was, perhaps, most abundant in 1948, and one specimen was taken in that year from the Moray Firth, though its presence there must be regarded as distinctly unusual.

Spadella cephaloptera (Busch) is widely distributed throughout the Scottish area as a bottom-living form and is therefore not included here as planktonic.

There are several other species which occur only occasionally in the Scottish plankton either as individual specimens or in small numbers in specialized localities: for convenience these may be termed unusual species. They are as follows.

Sagitta elegans arctica Aurivillius, which has occurred in several years in the Faroe-Shetland Channel associated with the community characterized by *Eukrohnia hamata* and *Calanus hyperboreus*.

Sagitta hexaptera d'Orbigny, a warm deep water species, which was found in the Faroe-Shetland Channel in 1935, 1939 and 1948 in conditions usually associated with *S. lyra*.

S. planctonis Steinhaus. This species was not recorded until 1948 when several specimens were taken in areas over deep water off the edge of the continental shelf west of the Hebrides. As this area has not yet been extensively sampled by the Scottish research vessels, it may be more common there than the number of records to date would indicate.

S. bipunctata Quoy & Gaimard, which was found off Cape Wrath in March 1949. There has been a good deal of controversy about this species, until the past decade or two *S. elegans* and also *S. setosa* were frequently recorded as '*bipunctata*'. *S. bipunctata* is normally a warm water species and the occurrence of three specimens off Cape Wrath— $58^{\circ} 50' \text{N}$. $6^{\circ} 26' \text{W}$.—on 2 March 1949 is of considerable interest. Apart from misnomers, these are believed to be the first records of this species in Scottish plankton samples. Although generally recognized as of widespread distribution in the warmer seas, it has previously been recorded only as far north as the Azores (Burfield, 1930).

The Cape Wrath specimens, which are 9, 10 and 13 mm. in length, are all immature and the *vesiculae seminales* are only slightly developed so that their mature shape and position cannot be ascertained with certainty. They appear to be nearer the posterior fin than described by Ritter-Zahony (1911) and Burfield (1930), but agree with the description by Michael (1911), and they might well extend to the tail fin when fully mature.

Like Michael (1911) and Burfield (1930), I find no trace of a local epidermal thickening between the *vesiculae seminales* and the posterior fin such as that described by Tokioka (1939) from Japanese specimens and by Thomson (1947) from Australia. The present specimens, except for maturity, resemble some from Bermuda and South Africa that I had the opportunity of seeing, through the courtesy of Mr F. S. Russell, and Dr S. G. Gibbons.

Krohnia (Eukrohnia) subtilis (Grassi). A single specimen of *K. subtilis* was taken in a subsurface net (50 m. depth) from $56^{\circ} 50' \text{N}$. $90^{\circ} 50' \text{W}$. some 80 miles west of the Hebrides, where the depth exceeded 1800 m. This record is also believed to be the first from the Scottish area. Many bathypelagic copepoda, together with *Sagitta planctonis*, *S. lyra* and *S. maxima*, and other deep-water species, were also found at this station.

There are several other species that might be expected to occur occasionally off the west coast of Scotland and in the Faroe-Shetland Channel, but which have not so far been identified from plankton samples taken by Scottish research vessels. They are *S. macrocephala*, *S. decipiens* and *Eukrohnia fowleri* (see Russell, 1938, and the literature referred to therein).¹

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¹ Since writing this, both *Sagitta macrocephala* and *Eukrohnia fowleri* have been taken in oblique hauls from 1000 m. and 1500 m. to the surface in positions west of the Hebrides in June 1949.

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THE STRUCTURE AND MODE OF LIFE OF THE PYRAMIDELLIDAE, PARASITIC OPISTHOBRANCHS

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(Text-figs. 1-12)

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INTRODUCTION

The family Pyramidellidae makes a brave show in fauna lists and similar publications: Winckworth (1932) includes at least forty-one species in his list of British marine molluscs, and Ankel (1936) mentions twenty-seven in the fauna of the North and Baltic Seas. Of the thirty-nine different species, however, of which descriptions are given by Jeffreys (1867), one-third are identified only in respect of their shell characters and nothing at all is said of the appearance of the soft parts of the mollusc; while many volumes, such as the fauna list of the Marine Biological Association (1931), enter their records of species of *Odostomia* as 'dead shells only'. It is thus largely true that the pyramidellids are a conchologist's group and that a marine naturalist of considerable experience may not have set eyes upon a member of that family. This is to some extent explained by the fact that all the Pyramidellidae are small, not to say minute, and are not conspicuously coloured, and by the fact that many of them are not particularly common. But one other factor which contributes largely to the general obscurity surrounding this group of gastropods is that each species appears to have its own extremely specialized habitat, and in ignorance of this collecting will not produce any specimens of that particular sort. It has long been known that one species, *Odostomia eulimoides* Hanley, is to be found 'chiefly (if not only) on the ears of *Chlamys opercularis* and *Pecten maximus*', in Jeffreys's words, and this habit of restricting its occurrence to

one special location appears to be a characteristic of every species of the family. Each one lives in definite relationship to another animal, usually a sedentary polychaete or mollusc, and, presumably, were one to know the particular animal in relation to which each species lives, one could then search for the pyramidellids with fair measure of success. This habit has long been known for a few species—since Jeffreys's time (1867) for *Odostomia eulimoides*, and since 1914 for *O. scalaris* Macgillivray (= *rissoides* Hanley), when Pelseneer (1914) described this species as living in the neighbourhood of, or actually on, the shell of *Mytilus edulis*. It was also known as a result of work by Pelseneer (1914), Ankel (1938), and Rasmussen (1944) that these molluscs probably fed on the animals on which, or in the neighbourhood of which, they dwelt, but the details of the feeding process and of the alimentary system were not known. All that appeared certain was that the Pyramidellidae possessed no radula, for which reason Thiele (1929) classified them in the stirps Aglossa of his order Mesogastropoda.

That this classification might not be accurate was first indicated by Thorson (1946), commenting on Lebour's description (1932) of the larvae of *Odostomia*, which she claimed were unmistakably recognizable by reason of their sinistral shell, which in many species persists throughout life on top of the dextral adult shell. This sinistral larval shell, according to Thorson (1946), is regularly found in the larvae of opisthobranchs, and on this basis he suggests, reviving the much older ideas of Mørch (1865), that the Pyramidellidae are, if not actually opisthobranchs, very closely allied to them. This, however, has been denied by Pelseneer (1899).

The work described in the following pages, carried out at the marine laboratories at Plymouth and Cullercoats as well as in London, shows how the gut of *Odostomia* species is built and functions, describes the habitat and feeding of a number of different species, the main plan of the mantle cavity, nervous and reproductive systems, the breeding habits and veligers, and concludes, on the basis of this, that the Pyramidellidae should in fact be classified along with the opisthobranchs.

We wish to record our thanks to Mr F. S. Russell, F.R.S., and to Dr H. O. Bull for the facilities provided at Plymouth and Cullercoats respectively, to Mr R. Winckworth for checking identifications, and to Birkbeck College for a grant.

The following description, unless otherwise stated, applies to the genus *Odostomia* and to the genus *Chrysallida*.

EXTERNAL FEATURES

The Pyramidellidae are all small animals and, so far as external appearances are concerned, they look like any typical monotocardian prosobranch in that the visceral hump is large, wound in a dextral spiral, and enclosed in a stout,

calcareous shell into which head and foot may be completely withdrawn when the animal is disturbed. The mantle cavity is like that of any prosobranch, too, facing anteriorly and opening to the exterior over the head and almost equally to left and right. There is no clear tendency for the mantle to extend beyond the mouth of the shell except at one point on the right, where it is produced into a short spoon-shaped process.

The foot is short, with a creeping sole, broad anteriorly and tapering posteriorly where, dorsally, it carries a lightly coloured operculum, which sends several tooth-like processes some distance into the flesh of the foot as if to provide greater anchorage for the columellar muscle. Along the mid-ventral line of the sole posteriorly there is a deep longitudinal groove and at the anterior end, which is drawn out laterally into slight points, lies the mouth of the pedal mucous gland, which is well developed, not only filling the central part of the foot with mucous cells but thrusting further lobes into the head, where they lie around the front end of the alimentary canal and the nerve ring. The lateral surfaces of the foot show no outgrowths of any kind.

The foot is covered with a columnar epithelium, strongly ciliated over the entire sole, but with only scattered ciliated cells over the remainder of the surface. Under the epithelium lie large numbers of gland cells, the secretion of which is not mucous. These are spherical in shape, 20μ in diameter, and they lie in the connective tissue of the foot. Their contents are finely granular and they are discharged by ducts passing between the epithelial cells. In two special areas a second type of gland cell occurs, packed together so as to produce a lateral glandular streak on either side of the foot parallel to the edge of the sole, but placed a little more dorsally, in the same position as described by Yonge (1947) for *Patella*. The cells (Fig. 2, GC) here are also spherical and lie in the subepithelial connective tissue, opening to the exterior by ducts running between the epithelial cells, but their contents consist of large numbers of spherules which stain strongly with basic stains when ready to be discharged. Frequently smaller granulations (G) lie at the centre of the spherules. A basket-work of muscles (MS) lies around each cell, the fibres running from under the epithelium to end in vertical bundles of muscle (DMF) deeper in the foot, and it seems probable that the contents of the gland cells are squeezed out through the ducts by contraction of this muscular network. In the epithelium through which the cells of the lateral glandular streak open lie scattered cells (CC) bearing bundles of long cilia (30μ). These are perhaps sensory in nature as similar ones appear regularly in the epithelium which covers the surface of the cephalic tentacles (see below), and their presence would suggest that the lateral glandular streak is some kind of sensory organ.

From the opening of the pedal mucous gland the anterior dorsal surface of the foot curves upwards and backwards on to the head, but before that part of the body is reached the foot projects outwards into a thin fold running transversely from one side of the body to the other and slightly indented in the

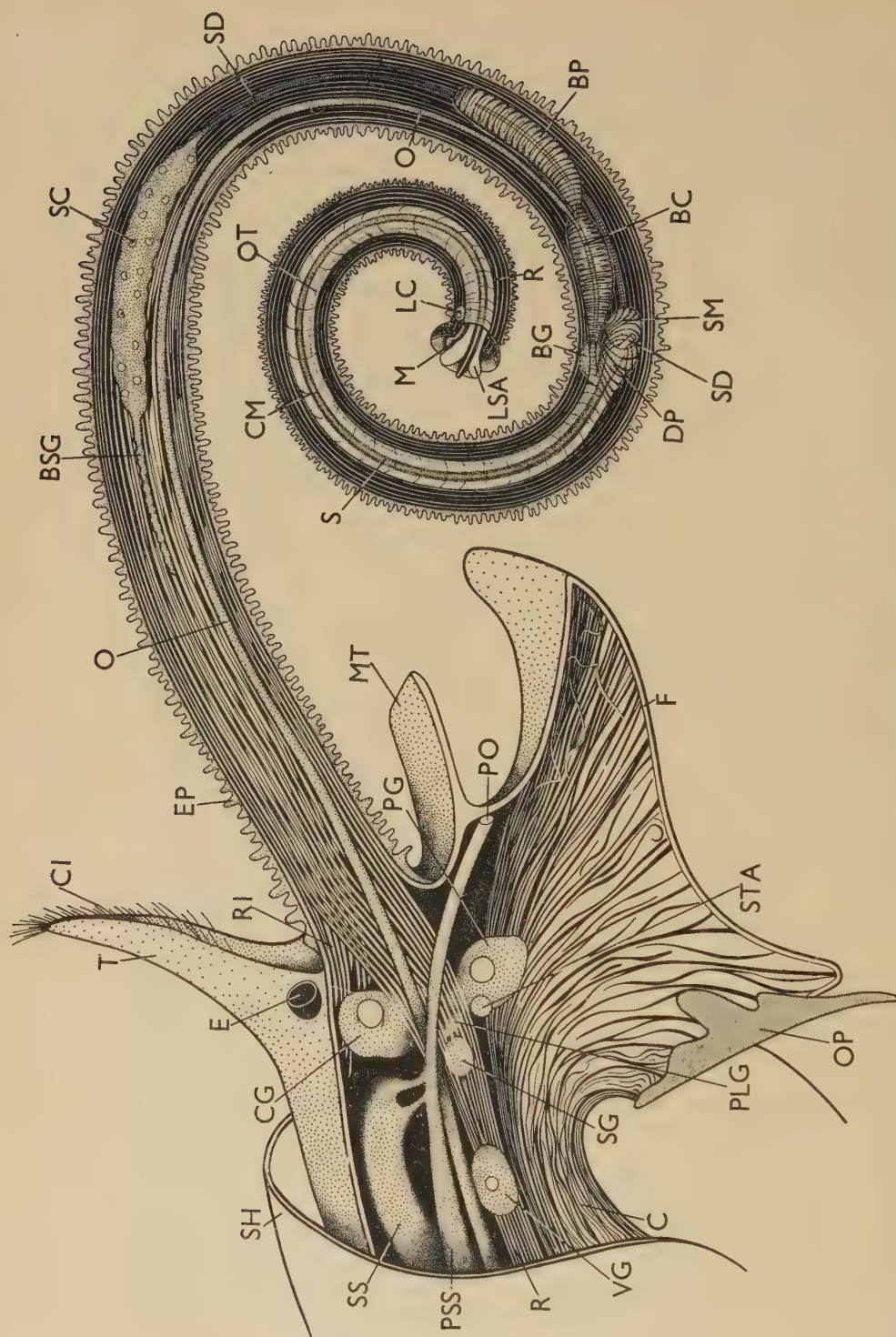


Fig. 1. *Odostomia unidentata*. Sagittal half of the anterior end of a specimen protruding head and foot from the shell, and with the proboscis everted. The position of this is diagrammatic. The haemocoel is black. $\times c. 96$. BC, buccal cavity; BP, buccal pump; BSG, bladder of salivary gland; C, columnar muscle; CG, cerebral ganglion; CI, sensory cirri; CM, circular muscles; DP, dorsal pouch of buccal cavity; E, eye; EP, epithelial papilla; F, foot; LG, labial commissure; LSA, lip of stylet aperture; M, mouth; MT, mentum; O, oesophagus; OP, operculum; OT, oral tube; PG, pedal ganglion; PLG, pleural ganglion; PO, opening of penial sheath; PSS, penial sheath; R, retractor muscle of introvert; R1, protractor muscles of introvert; S, stylet; SC, cell of salivary gland; SD, salivary duct; SG, suboesophageal ganglion; SH, shell; SM, muscles moving stylet; SS, sperm sac; STA, statocyst; T, tentacle; VG, visceral ganglion.

mid-line: this is the mentum (Fig. 1, MT), a structure also to be found in the family Eulimidae (Kœhler & Vaney, 1908). At first sight it looks as if it were a snout, with the mouth at its tip, and the habit which *Odostomia* has of carrying it in front of the tip of the sole of the foot, in contact with the substratum, lends support to that view. Nevertheless, this structure is pedal, carries no openings at its apex and has no special histological characteristics, resembling in all respects other unspecialized parts of the foot. Ventral to this mentum, slightly to the right of the mid-line, is an opening (Fig. 1, PO), that of the penial sheath.

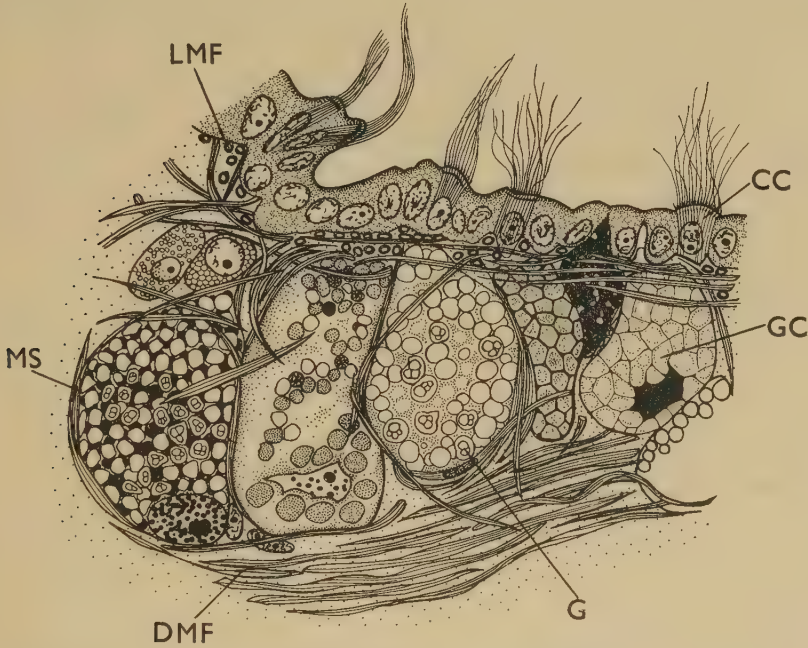


Fig. 2. *Odostomia unidentata*. Transverse section through lateral glandular streak. $\times 600$. CC, ciliated cell; DMF, dorsoventral muscles of foot; G, granulation; GC, gland cell; LMF, longitudinal muscles of foot; MS, muscles discharging secretion.

The head carries a pair of tentacles (T), a pair of eyes (E) and a pair of apertures—and there is something unusual about each of these structures. The tentacles are shaped like the ears of a donkey or rabbit, with a concave outer surface and, like the ears of these animals, they may be moved so that the concavity may face in a variety of directions. The cavity is lined by an epithelium, reminiscent of that covering the lateral parts of the foot: the cells are mainly covered with short, strong cilia which create a current of water that swirls into the concavity of the tentacle from the outer side and passes towards the mid-line as noted by Alder (Jeffreys, 1867). When *Odostomia* is examined alive and feeding these tentacles are seen to project forwards from the head,

diverging slightly, with the concavities facing forwards, downwards and slightly outwards. The movement of particles in the water shows that the cilia on the grooves draw a strong current in from over a considerable volume of water. Examination of living molluscs will also show the presence of long spike-like cilia projecting motionless from the surface and edges of the groove, most abundantly near the summit of the tentacle, which often appears fringed as a result. These, too, were noted by Alder. They seem to be sensory in nature and are probably compound structures, made by the functional fusion of many cilia, since in sections of fixed material no comparable cilia may be seen in these regions, whereas large tufts of separate cilia are to be found with similar length and distribution. The same interpretation may probably be applied to the tufts of cilia described on the sides of the foot (Fig. 2).

In the connective tissue below the epithelium of the tentacles there occur large numbers of spherical gland cells opening by ducts lying between the epithelial cells, similar to those occurring over the foot. They are sufficiently numerous for the margins of the spheres to be practically in contact. The centre of the tentacle is filled with a padding of connective tissue round the muscle strands responsible for the tentacular movements, but in addition to this there are lobed groups of cells that seem to be nervous and of the nature of small ganglionic masses. They arise at the base of the tentacle from a number of small nerves originating in the cerebral ganglia and they lie, mixed with the tentacular muscles and glands, in irregular masses under the epithelium, especially abundant at the base of the tentacles, in the proximity of the eyes and of the optic and cerebral ganglia, decreasing in size and number as the apex of the tentacle is reached. Their connexions (if any) with cells in the epithelium have not been discovered, but their certain relationship to the rich innervation, and their close contact with the epithelium of the tentacle suggest forcibly that they are part of a sensory mechanism. In conjunction with the stream of water which is maintained through the tentacular groove these cells and nervous masses would make the tentacles of a pyramidellid important organs for the sampling of the water in the neighbourhood of the animal.

The eyes of *Odostomia* and other pyramidellids lie close together under the skin of the head on the *median* side of the tentacles, instead of on stalks at the outer side as is usual in prosobranchs.

On the under side of the head lies the inconspicuous mouth. The opening of the penial sheath (Fig. 1, po) is present in every individual, as all these pyramidellids are hermaphrodite. From it a ciliated tract runs backwards along the right side of the head, ventral to the base of the tentacle, on to the floor of the mantle cavity to end at the single genital opening. Occasionally this tract is elevated above the general surface of the foot and head, over which it runs, so as to form a slight ridge. This is variable and is due to local muscular contractions.

Although the mantle cavity is narrow in a dorsoventral direction it is, never-

theless, capacious, because of its width and the length to which it extends along the front of the visceral hump. To it discharge (i) the genital duct, in *Odostomia* about one-third of its total depth inwards from the mouth, lying at the bottom of a deep groove on the floor to the right near the mid-line; (ii) the kidney, by a minute pore projecting downwards from the roof, at the apex of a small papilla still deeper in the cavity; and (iii) the anus, a very small opening at the innermost end of the mantle cavity, on the floor, at the extreme left side (Fig. 11, A).

The inner half of the mantle, which forms the roof of the inner part of the mantle cavity, is more or less equally occupied by two structures—the kidney, which, as in the small gastropods described by Fretter (1948), lies entirely in this position and not in the visceral mass at all, and which is placed immediately anterior and dorsal to the anus, lying on the left side; and, secondly, a vast glandular field, which extends on the right side to the innermost end of the mantle cavity. A narrow line of epithelium without glandular cells runs between the left edge of this area and the kidney, and a similar strip occupies the extreme right hand of the mantle cavity, so that the glandular region is clearly separated from neighbouring structures. Along its right-hand edge there runs a narrow strip—only about a dozen cells in breadth—of strongly ciliated epithelium, and this runs forward from the anterior end of the main glandular region to the mouth of the mantle cavity, which it reaches dorsal to and to the right of the head.

The inner half of the floor of the mantle cavity is less complex in its arrangement than the roof. The anus and genital opening lie on it and from the lips of the anus a glandular streak stretches at first across the mantle cavity from left to right and then forwards along the floor, passing to the right of the genital opening, and keeping more or less directly under the glandular area which lies on the roof of the mantle cavity, but clearly separated from it by the non-glandular strip of cells along the extreme right-hand margin of the mantle cavity. As in the dorsal area a strip of ciliated cells runs along the right-hand edge of the ventral glandular region, the two lying more or less one above the other, and this ciliated strip, too, continues to the mouth of the mantle cavity. Occasionally the two strips appear to be connected one to the other at the innermost end of the mantle cavity, but in other individuals they are clearly separate. The general arrangement is similar to what was described by Fretter (1948) in *Omalogyra* and *Rissoella*.

The outer half of the mantle is simpler than the inner and contains no special organ apart from the extensions of the ciliated strips already referred to. At no other place is the epithelium which covers it ciliated, and except at the mantle edge there are no gland cells; the epithelium is low, cubical or even squamous in character and permits ready exchange of respiratory gases between the water in the mantle cavity and the very rich bed of blood vessels which the mantle itself contains. This region would also appear to be a site of excretion, as numbers of amoeboid cells, the cytoplasm of which is loaded with spherules,

may be seen in the blood spaces and in the act of passing out into the mantle cavity. These seem to be a source of great attraction to ciliates which regularly occur in large numbers in the mantle cavity of *Odostomia*, since wherever one of these cells is found in a pallial blood space or making its way through the epithelium of the mantle, there will always be found at least one ciliate hovering directly over it, presumably for the sake of ingesting the material which the cells are about to empty into the mantle cavity.

At the mantle edge a greater degree of histological differentiation has occurred: the cells of the epithelium are columnar and there are considerable numbers of gland cells lying in the pallial thickness. Some of these are simple mucous cells, but there are others the nature of the secretion of which is unknown. The greatest degree of histological complexity, however, occurs in the two glandular areas, dorsal and ventral. The former is composed of two types of gland cell: one is a mucous cell (60μ), tall and wedge-shaped; whilst the second secretes spherules of a material which stains very darkly with iron haematoxylin when the secretion is being elaborated, but much less intensely at the time of liberation. These cells are of the same height as the mucous cells but are columnar in shape. In some parts of the field the two types occur in equal abundance and more or less alternately, but there are other regions, where mucous cells are most abundant, or even the sole type found; whereas along the edge of the glandular area that abuts upon the kidney mucous cells are practically never to be seen and the cells are all of the other type. This is also the kind of gland cell which predominates in the ventral fold, though here, too, mucous cells are mingled with them and, in the neighbourhood of the lateral tract, are more frequent. In the neighbourhood of the genital opening there occurs a grouping of a third variety, the cytoplasm of which is crammed with vacuoles, each filled with a mass of brown-coloured material. These are packed so tightly together that they are compressed into irregular, polygonal shapes staining erratically with iron haematoxylin. Whether they are ever shed, or whether they accumulate in the cells is not known, but they make a conspicuous linear mark, usually brown-orange or pink in colour, on the body of the mollusc—the anal gland of Lebour (1932), or larval kidney of Rasmussen (1944)—which is often visible by transparency through the shell, as in *Rissoella* Fretter (1948).

THE ALIMENTARY CANAL

The aperture which lies on the under side of the head is not the true mouth, but merely the opening of an introvert at the base of which the true mouth is placed, so that the animal is provided with a proboscis of the acrembolic type. When retracted, the introvert is flung into an S-shaped loop, the anterior end passing through the nerve ring, and the bulk of the loop coiled posteriorly in the haemocoel. At its innermost end lies the mouth, which is placed in all pyramidellids on a circular sucker. The sucker is shaped rather like a candle-

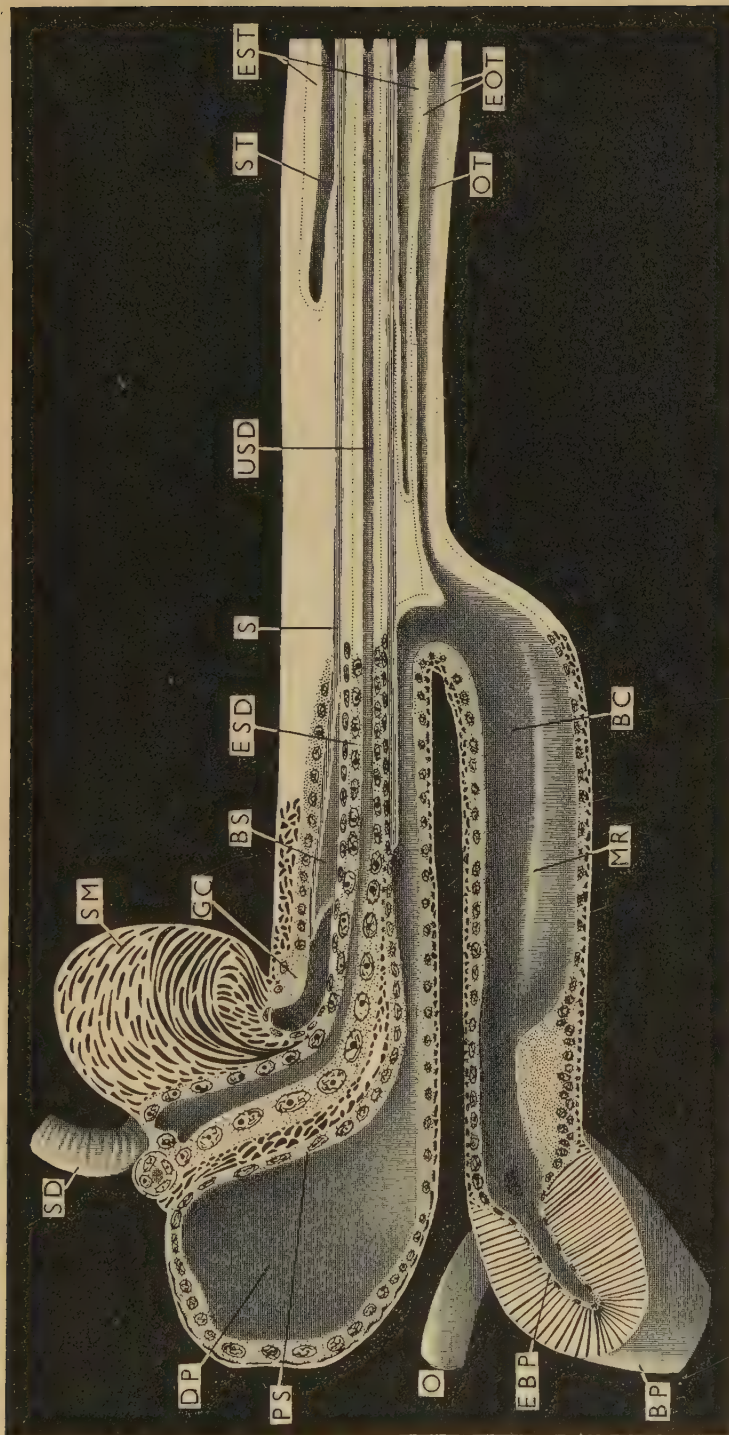


Fig. 3. *Odostomia*. Stereogram of a sagittal half of the base of the stylet and associated structures. $\times 600$. BS, base of stylet; EBP, epithelium of buccal pump; EOT, epithelium of oral tube; ESD, epithelium of salivary duct; EST, epithelium of stylet tube; GC, gland cell; MR, muscular ridge; rs, projection containing salivary ducts; ST, stylet tube; USD, united salivary ducts. Other letters as in Fig. 1.

stick, with an elevated central region as well as raised edges. In *Odostomia* spp. the mouth (Figs. 1 and 4, M) lies about half way between the centre and the edge of the sucker on the ventral side and is a narrow slit-like opening crescentic in shape. In addition to this opening there is a second lying in the centre of the sucker, with raised lips, and corresponding to the part of the candlestick into which the candle would be placed: this (Fig. 4, SA), as will be shown later, is merely a separated portion of the mouth, through which the animal can thrust a sharp spike-like stylet.

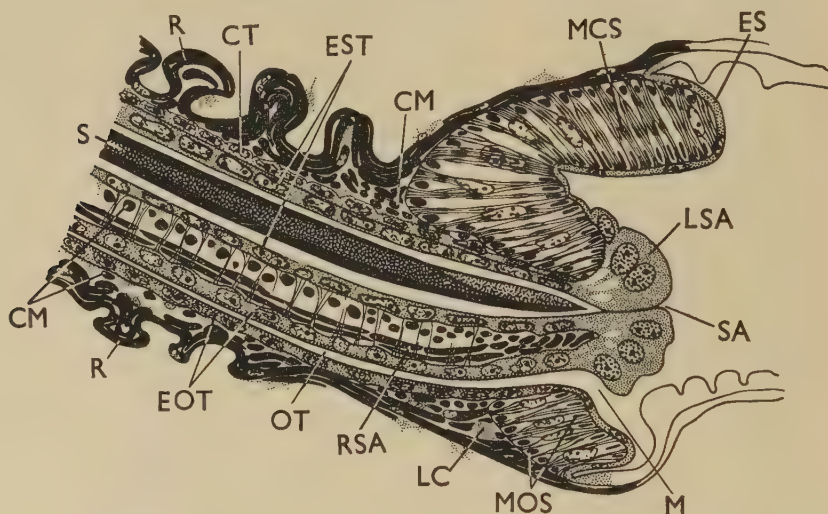


Fig. 4. *Odostomia plicata*. Longitudinal section through the mouth and initial part of the alimentary canal. $\times 600$. CT, connective tissue; EOT, epithelium of oral tube; ES, epithelium over sucker; EST, epithelium of stylet tube; MCS, muscles arching sucker; MOS, muscles flattening sucker; RSA, retractor muscle of lips of stylet aperture; SA, stylet aperture. Other letters as in Fig. 1.

From the sucker there extends inwards an elongated initial section of the alimentary canal which will be shown later to be the oral tube. The main channel in this is the space (Figs. 1, 3 and 4, OT), exceptionally narrow in a dorsoventral direction, which runs backwards from the mouth. Near its inner end the oral tube gives off a large, dorsally placed, blind pouch (Figs. 1 and 3, DP), which is part of the buccal cavity, and then its main channel turns towards the remainder of the buccal cavity and the oesophagus (Figs. 1 and 3, O). From its mid-dorsal point there projects into the pouch a long finger-like process (Fig. 3, PS), along the centre of which runs a single duct (Fig. 3, USD) formed by the fusion of the two ducts (SD) from the pair of salivary glands. The wall of the pouch into which this structure projects is, at the innermost end, a naked epithelium of rather flattened cells which is reflected on to the surface of the projection carrying the ducts of the salivary glands. Over a considerable area

of the ventral wall of the pouch and, to a lesser extent dorsally, the cells are frequently mucus-secreting, whilst in the neighbourhood of the connexion to the rest of the buccal cavity, the epithelium is cuticularized, this production

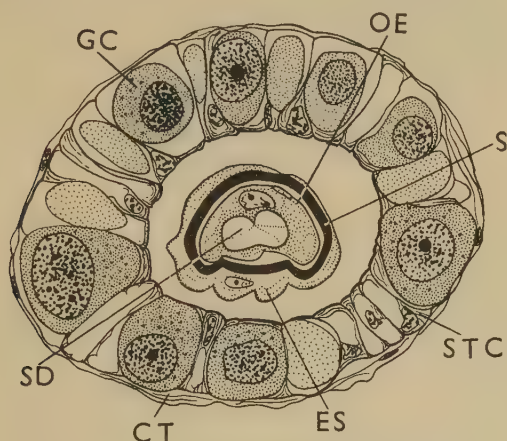


Fig. 5. *Turbonilla jeffreysii*. Transverse section through the stylet and oral tube. $\times 600$. CT, connective tissue; ES, epithelium around stylet; GC, gland cell; OE, outer epithelium; S, stylet; SD, salivary duct; STC, supporting cell.

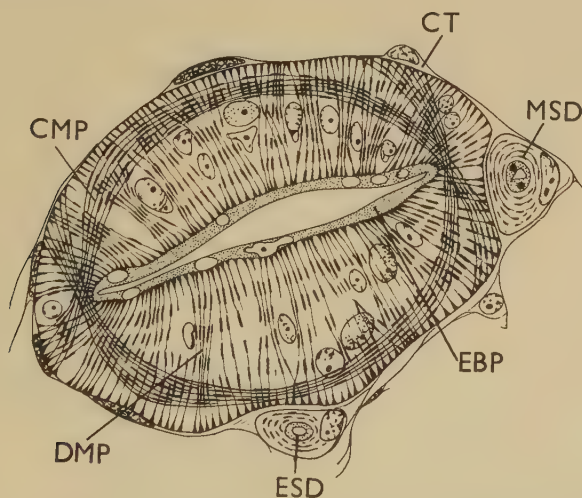


Fig. 6. *Odostomia lukisii*. Transverse section through the buccal pump and salivary ducts. $\times 600$. CMP, constrictor muscles of buccal pump; CT, connective tissue; DMP, dilator muscles of buccal pump; EBP, epithelium of buccal pump; ESD, epithelium of salivary duct; MSD, circular muscles of salivary duct.

of cuticle spreading along the dorsal wall of the pouch to the region of the narrow belt of mucous cells near the origin of the salivary process, but affecting the lateral walls to a lesser extent. The cuticle remains attached to the underlying epithelium dorsally and dorsolaterally, where the histological picture

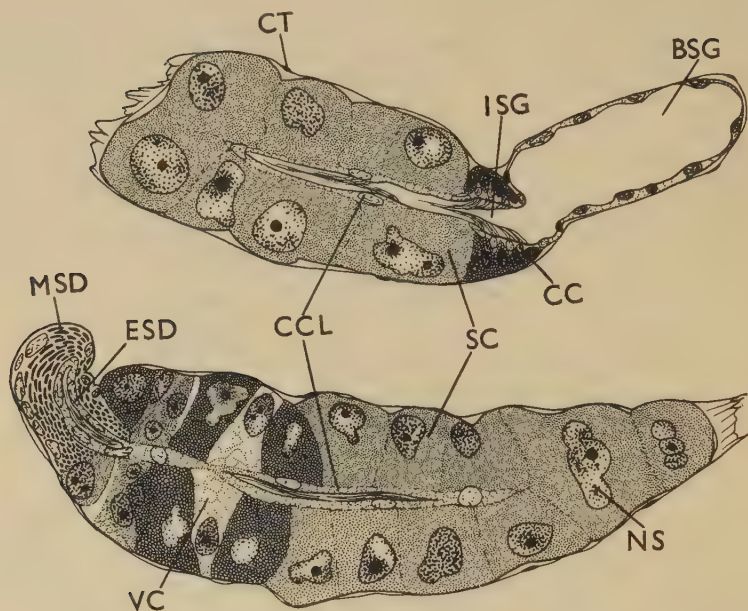


Fig. 7. *Odostomia lukisii*. Longitudinal section through the salivary gland. $\times 600$. BSG, bladder of salivary gland; CC, ciliated cell; CCL, ciliated epithelium of lumen; CT, connective tissue; ESD, epithelium of salivary duct; ISG, intermediate section of salivary gland; MSD, circular muscles of salivary duct; NS, nucleus of secreting cell; SC, cell of salivary gland; VC, vacuolated cell.

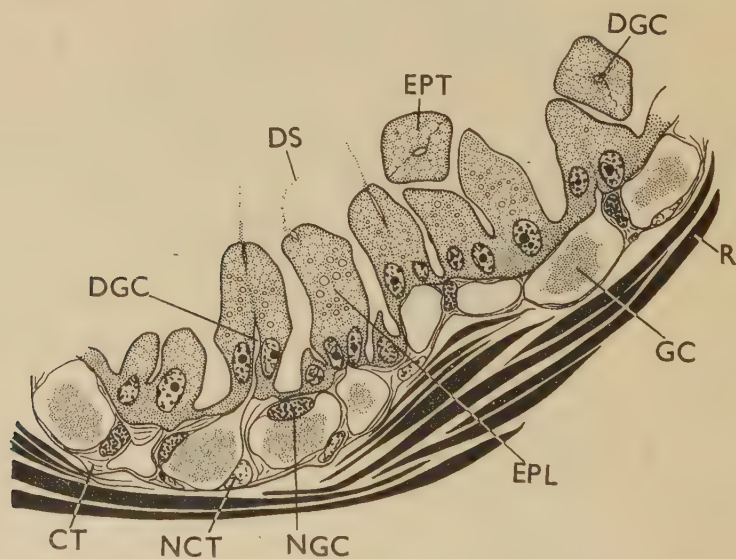


Fig. 8. *Odostomia unidentata*. Longitudinal section through a portion of the wall of the introvert. $\times 600$. CT, connective tissue; DGC, duct of gland cell; DS, secretion discharged to lumen; EPT, epithelial papilla in transverse section; GC, gland cell; NCT, nucleus of connective tissue cell; NGC, nucleus of gland cell; R, retractor muscles of introvert.

shows obviously that it is being secreted, but more ventrally it grows freely into the cavity of the pouch, losing contact with the epithelium, and embracing, as it does so, the long projection in which the salivary ducts are running. The two edges of the cuticle actually grow around this until they meet mid-ventrally in the cavity of the pouch near its mouth. In this way the common salivary duct, lying in the long process which grows out from the innermost part of the wall of the pouch, comes to be enclosed in a tubular cuticular sheath which is being continually added to at its base dorsally and dorsolaterally. On reaching the anterior end of the pouch, in *Odostomia*, this tubular cuticular structure plunges into the dorsal wall and runs for a short distance through the muscles and connective tissue of that wall. Soon, however, it emerges into a second space and runs along this to the sucker, where its anterior tip has already been described as projecting from the more dorsal of the two apertures which are placed thereon. At the base of this outer cavity the epithelium which lines it is reflected over the surface of the stylet, but this layer of cells is soon lost, and the stylet then lies naked in the cavity.

The epithelium which lines the oral tube (Figs. 3 and 4, EOT) is not remarkable in most places: it is a low cubical, almost squamous, epithelium with gland cells restricted to the dorsal wall of the space in which the stylet lies. These are mainly mucous, though a few secreting chromophile granules also occur. Sometimes these cells and the connective tissue cells around them lie under the dorsal epithelium of this cavity in such a regular way as to suggest the presence of a second epithelium in that position (Fig. 4, CT). At the lips of the mouth, and at the opening dorsal to that, through which the stylet is projected, this epithelium turns outwards over the concavity of the sucker, where it forms a very low and featureless layer of cells (ES), continued at the margin into the epithelium that lines the introvert. Only around the edge of the stylet aperture in the centre of the sucker is there any change in the character of the cells: here they are greatly enlarged (LSA), with vacuoles at their base, and large nuclei placed centrally in a mass of dense cytoplasm, so as to form a thick and rather fleshy looking rim to the opening.

The cells which line the innermost part of the introvert are shown in Fig. 8. They are raised in groups at regular intervals to form papillae, so that when the proboscis is thrust out and the lining of the introvert becomes the outer epithelium of the proboscis, it has a furry appearance (Fig. 1). Each papilla, in *Odostomia*, consists of three or four cells lying side by side; they are crushed together in the centre of the papilla where they abut against each other, but smoothly curved towards the exterior, so that each papilla rises from a narrow base, swells to a greater breadth and then tapers to a blunt apex. Up the centre of each papilla, through a long tube that seems to be formed along the line of meeting of the cells, runs a duct (Fig. 8, DGC) from a subepithelial gland placed in the connective tissue of the wall of the introvert (GC); and this opens by a minute apical opening to the lumen of the introvert when the

proboscis is withdrawn, or directly to the exterior if the proboscis be extended. The glands are spherical in shape and their contents are finely granular, reminiscent of those that lie in the outer surface of the head and on the sides of the foot—and as the introvert has presumably arisen by the in-pulling of a greatly extended snout the glands are in fact probably the same: it is their special way of opening in relation to the other cells of the epithelium which is of interest. The cytoplasmic organization of these cells, too, is in some ways specialized: the nuclei are always large and placed basally side by side in the narrow neck of the papilla. The cytoplasm is dense and contains a number of small spherules lying in irregular vacuolations which do not stain differently from the other parts of the cytoplasm, but the most superficial layer is distinctly denser than any other part and after staining with mucicarmine it has frequently a pinkish tint. On some occasions, too, it has appeared as if the cortical region were striated. In the parts of the introvert lying nearer the external opening the characteristic arrangement of papillae is gradually replaced by an ordinary columnar epithelium, the height of which does indeed vary somewhat from spot to spot, but not in the regular way which has just been described. The cells are all of similar height, their cytoplasm not specially organized and the number of gland cells reduced and without any noteworthy relationship to the others.

Underneath the epithelium of the buccal region lies a complex array of muscle fibres, many of which are part of the mechanism for the retraction of the extended proboscis. The fibres which are responsible for the greater part of the retraction (Figs. 1 and 4, R) are set on the edge of the sucker, curve round its inner face and then travel as a muscular sleeve around the stylet and oral tubes towards the inner end of the latter. The fibres of the sleeve are not, however, all parallel to one another, but gradually converge to form a closely knit bundle of muscle, lying to the ventral side of the gut. This then runs up the visceral hump alongside the columellar muscle, and is inserted like that on the columella of the shell, high up the spiral of the visceral hump. When the proboscis is extended the retractor muscle is of course relaxed and stretched taut, running alongside the gut along the whole length of the proboscis, through the nerve ring and thence on to the columellar muscle; when it is contracted it is flung into a large S-bend, one of the angles of the S being in the neighbourhood of the buccal ganglia, the other, the more distal, near the origin of the stylet. The fibres during their course from the columellar muscle to the ganglia, and then on to the second bend, are straight when contracted; those from the second bend to the sucker, however, are flung into great loops when in the same state. Subsidiary bundles of muscles run from the wall of the introvert directly to the body wall (Fig. 1, R I). All these bundles run through the nerve ring when the proboscis is retracted, and they will therefore help in its extension. This, however, is presumably brought about mainly by the pressure on the blood in the haemocoel exerted by the musculature of the body wall.

In addition to the retractor muscles there are other, intrinsic, muscles of the gut wall which help in the movement of the stylet and presumably in the feeding movements as well. The latter are mainly due to circular fibres which constitute a muscular coat of considerable dimensions lying directly within the longitudinal sheet formed by the retractors. The thickness of the coat is less at the outer end, in the neighbourhood of the sucker, than at the inner end, near the dorsal pouch of the buccal cavity, where the fibres are elaborated into a muscular mass of great complexity around the base of the stylet and the point of entry of the salivary ducts. Here they are responsible for the movements of the stylet (Figs. 1 and 3, SM). Further bundles of circular muscle fibres lie around the oral tube (Figs. 1 and 4, CM) and are presumably involved in peristaltic movements affecting that region, whilst a bundle of longitudinal fibres which runs up to the lips of the stylet aperture (Fig. 4, RSA) would apparently pull these back, and help in this way to expose the tip of the stylet.

All the muscles so far described are unstriated.

The sucker, by which animals of this genus obtain a grip on the body of the creatures upon which they feed, is provided with musculature arranged in the same plan as in platyhelminths. There are three sets of intrinsic muscles involved. A series of cells runs through the depth of the sucker between its inner and outer surfaces (MCS), attached to the under side of the epithelial cells which cover the sucker in the latter position, and ending on a sheet of connective tissue in the former. When they contract, the degree of concavity of the sucker is increased and its grip augmented. Antagonizing these is a double set of circular muscles (MOS) which lie between the ends of the cells of the first set, one group just under the outer epithelium, the other just within the inner layer of connective tissue. All these muscle cells contain groups of fibrillae and these are all striated, though the striation appears to be less complex than in vertebrate muscle cells.

The main part of the buccal cavity continues behind the point at which the dorsal pouch (Figs. 1 and 3, DP) is given off. This section is histologically similar to that pouch, with part of the wall, dorsally, near the origin of the pouch, cuticularized, and the rest rich in mucous cells. These are especially abundant ventrally, where they form two longitudinal ridges, one on either side of the mid-ventral line. Anteriorly the space between these ridges is a narrow groove lined by cells which are not glandular, but at the innermost end of the cavity the ridges converge so as to obliterate the groove, though the type of cell which lies at this spot does not alter. A thin coat of circular muscle surrounds this.

The character of the gut changes abruptly at the hinder end of this section where an extremely muscular organ, the buccal pump (Figs. 1 and 3, BP), is developed. This is a short length of the gut divisible into two halves, with the oesophagus (Fig. 1, O) coming out ventrally near the middle, its point of attachment coinciding with a constriction separating the two halves. The

second half of the pump is therefore a caecum. Both parts, however, are identical in general plan (Fig. 6); they are flattened in a dorsoventral direction with a narrow central cavity. Their walls are very thick, by far the greatest part of this being due to the development of muscle fibres, and in general, they are very reminiscent of the structure of the sucker. The epithelium (EBP) which lines the pump is extremely low (2μ in height) and rests directly on the muscle of the wall. The bulk of this is formed of radial cells (DMP) fastened to the under side of the epithelium externally and to a sheet of connective tissue internally. Each cell, as in the sucker, has bundles of contractile fibrillae differentiated in its cytoplasm and these are all striated. Clearly, when these contract, they will give a strong and probably sudden pull on the epithelium, which will increase the dorsoventral diameter of the lumen of this part of the gut and so increase the volume. Antagonists (CMP) to this set of radial fibres are provided by transverse sheets of fibrillae, also striated, which run rather more than half way across each side of the cavity; their contraction will restore the cavity to its original volume.

Both these and the preceding section of the gut are closely linked with the salivary glands (Fig. 1, SC, SD), of which one pair is present. They lie freely in the haemocoel, though they may be attached to the body wall at their tip by fine strands of connective tissue or muscle. Each gland is connected to the gut by a long duct (Fig. 1, SD), and in the gland itself three distinct sections may be distinguished. The section lying next to the duct (Fig. 7) is composed of a series of large cells more or less quadrilateral in section. Their outer ends bulge slightly outwards against the layer of fine connective tissue (CT) that separates them from the haemocoel and it is noticeable, both in sections and in the intact gland, that the cells along one side alternate with those of the other. Almost all the cells have the same appearance—dense, even and darkly staining (iron haematoxylin) cytoplasm containing a large and irregularly lobed nucleus with a prominent nucleolus and many small granulations, the shape of the nucleus probably being an indication of intense metabolic activity (NS). In the few cells nearest to the ducts the cytoplasm is sometimes denser than in those farther away and the cells seem smaller and less well fitted together into an epithelium. An occasional cell (VC) will sometimes be distinct from all its neighbours and have a palely staining cytoplasm. Strictly speaking these are all subepithelial gland cells, because the lining of the central lumen is a layer of squamous epithelium bearing tufts of long cilia (CCL); these may be seen beating actively when a living gland is examined. The second section of the gland is brief and lies at the inner end of the secretory region: it is a short length where the same relationship of alternating ciliated and glandular cells occurs, but here the gland cells are small (ISG); they lie in the epithelium and stain even more intensely, whilst the ciliated cells (CC) are wedge-shaped with a long stalk connecting them to the basement membrane, and with their nuclei near the cilia. The lumen of the gland is broader and the cilia seem to beat with greater

vigour—though that may be merely an illusion occasioned by the fact that they have more space in which to beat. The innermost part of the gland is a thin-walled bladder (Figs. 1 and 7, BSG), lined by a squamous epithelium without cilia and without any obvious glandular appearance. The ducts are lined by an extension of the epithelium which lines the gland, but the greater part of the thickness of their wall is due to a great development of muscle cells containing circularly running fibrillae underneath the epithelium (Figs. 6 and 7, MSD). Like the fibrillae of the sucker and the pump these are striated. The two ducts run to the wall of the distal half of the pump, course along the lateral walls of that until the neighbourhood of the buccal cavity is reached, when they pass dorsally to enter the prolongation (Fig. 3, PS) which has already been described. There they unite, lose their muscular coat, and the single duct runs down the centre of the stylet to discharge saliva at the tip. When the proboscis is retracted the ducts coil irregularly in the haemocoel: when that is everted they are straight.

There are several points in the appearance of the salivary glands that suggest that there is a holocrine secretion occurring there without a restitution phase. The appearance of the cells at the two ends of the secretory part is unlike, though all the cells in a given region resemble one another. The cells are invariably larger at the inner part of the proximal region and invariably small and the epithelium less well compacted at the outer end of the same stretch, whilst if there were secretion going on from the entire gland, either in a rhythmic or arrhythmic fashion, now and again a section would show cells of the latter variety in other parts of the gland. Although we have no direct evidence on this point the appearance of the gland would suggest that there is a continual (or rhythmic or post-prandial) production of new cells from the middle region of the gland, and that the cells mature their secretion as they move towards the ducts along the outermost section of the gland, discharging it, and being destroyed in the process, when they reach the outer end of this, at the beginning of the duct.

The oesophagus (Fig. 1, O) originates from the inner end of the first half of the buccal pump (BP). It is a tube of capillary dimensions ($6-8\mu$) at its origin, but its diameter increases slowly and steadily as it runs up the visceral hump till it ends by opening into the stomach. It behaves like the ducts of the salivary glands, with which it is, in fact, closely associated: when the introvert is withdrawn into the body it coils in a close tangle with the salivary ducts; when the proboscis is thrust out it is stretched straight. The oesophageal walls are similar from one end to the other; the lining is a columnar epithelium, most of the cells having a very fibrillar cytoplasm. Occasional cells are probably glandular because they have numerous uniform, refringent spherules enclosed within them which are not dissolved in any fixative and are darkly staining. In *Turbonilla jeffreysii*, which feeds on coelenterates, a short terminal region of the oesophagus, of slightly larger diameter than the rest, has every cell filled

with nematocysts. It would appear that a certain amount of phagocytosis of food particles goes on here, and it may also be true of *Odostomia*, although the fluid nature of the food does not allow it to be made readily visible.

The stomach into which the oesophagus leads barely merits the name, as it cannot be distinguished from the digestive gland, a condition reminiscent of *Omalogyra* (Fretter, 1948). Except for the immediate neighbourhood of the oesophageal opening the entire epithelium is occupied by digestive cells and these are invariably packed full of brown spherules, which are darkly staining. A few cells in the digestive epithelium are of a different type: their nuclei are large and are, in fact, the only nuclei easily visible in sections, for they differ from the digestive cell in that the spherules in the cytoplasm are dissolved in acid fixatives. The gland occupies the greater part of the visceral hump, lying on the outer, convex, side of the spiral.

The intestine arises close to the oesophageal aperture and runs almost directly to the upper end of the mantle cavity, passing close to the vas deferens as it does so. The epithelium is ciliated. The anus lies on a small papilla.

THE VASCULAR SYSTEM

The vascular system of *Odostomia* is built upon the usual gastropod plan, but is modified in certain respects which may be of functional significance.

The heart lies in a pericardial cavity placed within the visceral hump, at the attachment of the mantle skirt on the left side, immediately proximal to the kidney, which opens to it in the usual way. The single auricle lies anterior to the ventricle, from which only one aorta emerges, at the inner end of the pericardial cavity. This vessel climbs up the visceral hump, on the concave side of the spiral, resting on the surface of the gonad which, in turn, is enwrapped by the digestive gland, so that it is plain that it corresponds to the posterior aorta of other molluscs. Longitudinal muscle fibres lie in the aortic wall. Near the apex of the visceral hump the posterior aorta opens into a haemocoelic space interpenetrating the lobules of the digestive gland and gonad. This drains into a second vascular channel which passes down the visceral hump on the outer, convex side so that it is wrapped around (save where it is pressed against the mantle) by digestive gland. At the level of the heart this expands into a vast haemocoelic space in which the pericardial cavity itself and the bulk of the structures in connexion with the reproductive system are placed, and through which the intestine and the upper end of the oesophagus also pass. From this chamber two vessels run forwards. Of these one passes into the head and then forwards and ventrally into the foot and it would therefore seem to correspond to the anterior aorta of other molluscs, although its central connexions are different. As it runs forwards, it lies immediately under the floor of the mantle cavity, raising that up so that it projects into the mantle cavity as a long ridge. In this part of its course it lies alongside the genital duct; on reaching the head

it dives deeply into the body, curving behind the nerve ring down the right side, so as to pass ventral to the pedal ganglia in the middle line of the anterior portion of the foot, and it ends here by opening into the main haemocoelic space of the body, occupying head and foot, in which are placed all the viscera of the animal except such as are situated in the visceral hump. The second vessel which leaves the upper haemocoelic space (the afferent pallial) runs into the roof of the mantle cavity and discharges blood into the numerous sinuses with which that part of the body is filled. The main pedal and cephalic haemocoelic cavities also drain into this region. Blood collects from the mantle into another vessel (the efferent pallial) which finally enters the auricle at the upper end of the mantle cavity. Before reaching that organ, however, the blood has to pass through a capillary bed on the wall of the kidney: in sections it may be seen that the outer wall of the kidney, especially where it is contiguous with the lining of the mantle cavity, is corrugated, and that the blood from the pallial sinuses must trickle along the tiny channels made by these corrugations in order to reach the main efferent vessel by which the auricle is gained.

The main course of the circulation is obvious. Blood is pumped by the heart up the posterior aorta to the organs placed in the visceral hump, and in minute, shelled gastropods like *Odostomia* it is clear that these are the only organs which will require a direct blood supply of this nature, since they are the only parts of the body continuously enclosed within a shell and so liable to suffer from oxygen lack. Under normal circumstances, with the body of the animal not shut inside the shell, head, foot and mantle will all act as respiratory surfaces, and it is unlikely that the blood will ever be significantly short of oxygen. Movements of the blood in the principal haemocoels are more likely to be produced by the movements of the head and foot and proboscis than by the beating of the heart, and, in particular, every time that the proboscis is everted—a process largely brought about by the hydraulic action of the blood in the cephalic haemocoel—and again when it is withdrawn, there must be produced powerful currents and disturbances in the vascular system. The special arrangement of the anterior aorta seems likely to be connected with this: its origin from a blood space instead of directly from the ventricle will ensure that this vessel can pour blood into the haemocoelic spaces of the head and foot as the proboscis is everted and, on the other hand, when the reverse process is taking place, the upper haemocoel will provide a storage place for the blood and will prevent damage to the heart that might have been difficult to avoid had that structure been connected directly to the haemocoel by the aorta.

Two other points in the vascular system deserve comment. One of these is the frequency of blood cells: these may be found in many of the vessels, but are most common in the spaces in the roof of the mantle cavity, in the anterior aorta and caught against strands of muscle in the chambers of the heart (Fig. 9). They are spherical in shape, with a round nucleus placed to one pole; the cytoplasm is not prominent apart from irregularly placed, scattered, or clumped

spherules which are invariably present, staining darkly with iron haematoxylin. These granulations are presumably excretory in nature, and one of the main activities of these cells would seem to be the transport of such particles to places where they may be cast out of the mollusc. This probably explains their abundance in the sinuses of the pallial region as it is mainly there, as recorded above (p. 500), that the cells have been seen in the process of discharging their contents to the mantle cavity. It is not certain whether they do not pass out themselves at the same time.

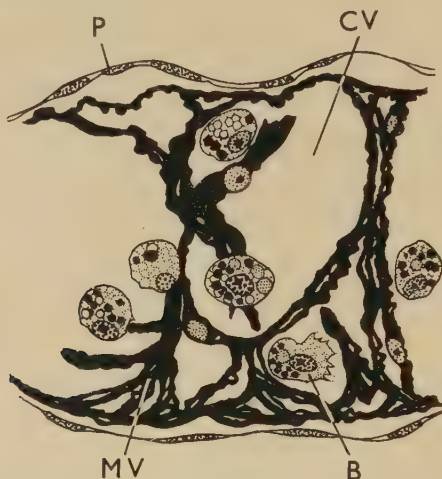


Fig. 9. *Odostomia unidentata*. Section through ventricle of heart to show blood cells. $\times 600$. B, blood cell; CV, cavity of ventricle; MV, muscles of ventricle; P, pericardium.

The second feature connected with the vascular system of *Odostomia* which should be noted is a differentiation of the wall of the anterior aorta where it runs forwards towards the head, alongside the terminal part of the genital duct. Here the cells which line the aortic wall abutting against the genital tract are specialized to form a thick pad of tissue. They are quadrilateral when seen in section, each with a large, darkly staining and granular nucleus; the cytoplasm is also granular. The nature of this group of cells is unknown.

THE NERVOUS SYSTEM

The ganglia of the nervous system of *Odostomia* are mainly concentrated into a ring which envelopes the proboscis, and also, quite unexpectedly, the penial sheath, and in which nine ganglia may be distinguished. In addition to the constituents of this ring two other paired ganglia may be observed in relation to the introvert, and a single unpaired one lies in the mantle on the animal's left side. A diagram of the nervous system is given in Fig. 10. Dorsal to the introvert lie the two cerebral ganglia (Figs. 1 and 10, CG): they are large, oval

in cross-section and the commissure between them so short that they are practically joined across the middle line. Anteriorly and ventrally they are drawn out into lobes (Fig. 10, LO, SL) which project considerable distances towards the eyes, the tentacles, and, to a lesser degree, the sides of the body between head and mentum. These merge into the ganglionic masses already described in these situations, and the main nerves for these regions arise out of these swellings.

Ventrally the cerebral ganglia are connected to the pedal ganglia (Figs. 1 and 10, PG), which are about equal to them in size, and, like them, are closely approximated, so that the commissure is hardly a separate structure. The cerebro-pedal connective is likewise rather short. On the postero-dorsal faces of the pedal ganglia lie the statocysts (Fig. 1, STA) in each of which is placed, as already noticed by Pelseneer (1899), a single calcareous statolith. At least four nerves leave each pedal ganglion and pass into the musculature of the foot. From each cerebral ganglion there also leaves a second connective, arising so close to the point of origin of the cerebro-pedal connective that it requires close observation to be sure that there are indeed two. A strip of muscle running from body wall to introvert, however, is regularly found separating the two structures, so that there is no real doubt that these are two independent nerves. The posterior of the two connectives runs to a small ganglion lying between the cerebral above and the pedal below, to which it is also linked by a further connective, and placed slightly posterior to both (Fig. 10, PLG). This is clearly the pleural ganglion on each side.

From the pleural ganglia there may be traced a visceral loop lying ventral to the introvert and not exhibiting any torsion. It is much abbreviated and does not extend far behind the rest of the nerve ring. On this loop three ganglia may

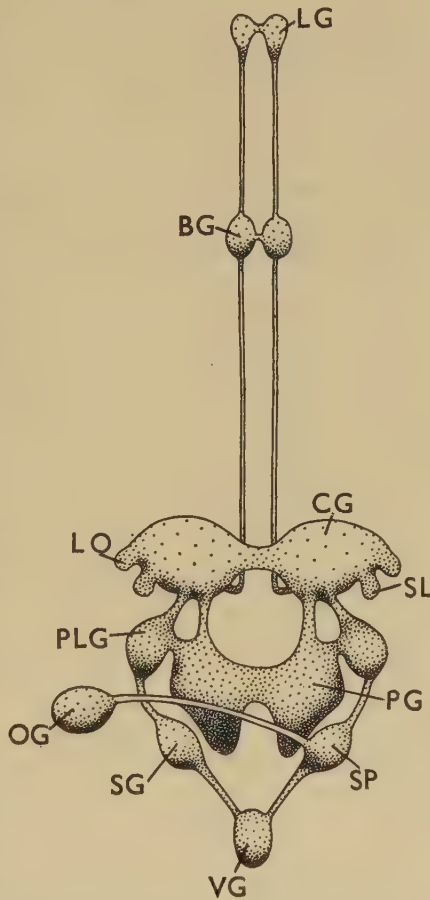


Fig. 10. *Odostomia*. Diagram of nervous system in dorsal view; the proboscis is supposed to be everted. LG, labial ganglion; OG, osphradial ganglion; LO, optic lobe; SL, sensory lobe; SP, supraoesophageal ganglion. Other letters as in Fig. 1.

be distinguished, and the most likely interpretation of these is that the one attached to the right pleural (Fig. 10, SP), is the supra-oesophageal ganglion, the one attached to the left pleural (Figs. 1 and 10, SG) is the suboesophageal ganglion, whilst the remaining ganglion would then represent the abdominal ganglion, a fusion of the two visceral ganglia (VG). It is, however, always possible that this is only one of the two visceral ganglia, the other having fused with one of the parietals as in *Aplysia*. Nerves arise from these that can be traced to the region of the genital aperture, kidney and heart so that their homologies are not in doubt.

There remain the ganglia which are not closely tied to the nerve ring. Of these one (Fig. 10, OG) lies on the floor of the mantle cavity on the left side and sends a prominent nerve to the roof of the mantle cavity. It is connected to the supra-oesophageal ganglion, and there is therefore little difficulty in homologizing this with the osphradial ganglion, although no specific osphradium can be recognized.

The other ganglia are two pairs lying in relation to the introvert, one pair (BG) in the cephalic haemocoel about half way along the introvert when that is retracted, close to the main retractor muscle of the proboscis. The second pair (LG) lies in the immediate neighbourhood of the sucker. Both pairs move outwards with the proboscis when that is extended (Fig. 1, BG, LC). The members of each pair lie closely side by side and are connected by short commissures. The other connexions of these pairs of ganglia have proved difficult to make out, but have now been seen both in dissections and in sections, a fact which must be emphasized a little, as not only do their connexions make their own homology certain, but they also help in establishing beyond any doubt the homologies of the anterior region of the alimentary canal. The pair of ganglia lying in the sucker are connected by a pair of nerves to the pair lying in the cephalic haemocoel on the main retractor muscle of the sucker. This pair of ganglia likewise gives off a pair of nerves which runs through the haemocoel towards the nerve ring. These nerves are particularly long because they must be able to stretch almost the entire length of the proboscis when that is extended. Like the fibres of the distal half of the retractor muscle, and like the ducts of the salivary glands and oesophagus, they are, for this reason, sinuously looped when the proboscis is retracted and straightened on the extension of that part of the body. On reaching the nerve ring the nerves pass dorsally and approach the cerebral ganglia, each nerve entering into a little lobe placed in a postero-ventral position on the cerebral ganglion. When one compares the plan of this part of the nervous system in a pyramidellid with the general plan of the gastropod nervous system, it is plain that only one interpretation of the homologies of these ganglia is possible: the pair which is connected to the cerebral ganglia must be the buccal ganglia, whilst those that lie in the sucker, that is in the lips of the mouth, must be the labial ganglia. The whole stomatogastric system must lie ventral to the main channel of the gut, though the

buccal commissure would be dorsal to a radular sac, from which it must be concluded that the side of the mouth on which the ganglia are placed is ventral.

REPRODUCTION

The pyramidellids are simultaneous hermaphrodites: ripe sperm and ova lie side by side in the same tubules of the gonad. The simpler requirements of the male reproductive system enable young individuals to function as males until the ova and the relatively enormous glands associated with egg laying are mature. Both types of gamete use the same ducts and are liberated into the mantle cavity through the same genital aperture. The path of the spermatozoa is, however, extended from here by the ciliated seminal tract which leads along the floor of the mantle cavity and around the base of the right tentacle to the penis.

Fig. 11 shows the disposition of the reproductive organs of a mature individual. From the gonad (H), on the columellar side of the visceral mass, a narrow though very distensible genital duct (GD), lined by a columnar ciliated epithelium, takes a somewhat sinuous course through the haemocoel towards the posterior end of the mantle cavity. Immediately after leaving the gonad it is distended with sperm (V), acting in this region as a vesicula seminalis; sperm are stored here even during a period of spawning, when the ova make their way, one by one, through the mass of ripe spermatozoa. From the vesicula seminalis the duct loops under the intestine (I) and describes a U-shaped bend around the posterior aorta before passing forwards to open into the pallial hermaphrodite duct (GO). Along the final part of its course it receives the openings of three glands which are concerned with the production of the egg masses. Two of these, the albumen gland (AG, DA) and the mucous gland (MGU, DU), open close to one another; the third opens near the entrance to the pallial duct and is a second mucous gland attaining a greater size than the first (MGL, OL). The white, flocculent lobes of the albumen gland tend to embrace those of the upper mucous gland. In both, as elsewhere in the genital system, the secreting cells in the epithelium alternate with small ciliated cells wedged between their distal ends (GC, CC). The secretion within the cells of the albumen gland is in the form of spherules which stain lightly with Heidenhain's haematoxylin and are embedded in a more deeply staining cytoplasm; in sections the secretion can usually be found in the form of a plug blocking the narrow duct which leads towards the genital aperture. The two mucous glands can not only be distinguished by a difference in size, but also by a difference in the staining properties of the component cells: those of the lower one respond to stains which are specific for mucus more readily than those of the upper. This distal gland is the last to appear in the development of the female system, but its growth is rapid and its lobes soon come to envelope the proximal end of the pallial duct, often extending halfway down its length.

The pallial genital duct is divisible into two regions: a proximal glandular part (GO) occupying about half of the length and expanding posteriorly as a commodious pouch, and a distal ciliated, conducting region which is more muscular. Running along the median wall of the former, and as a less conspicuous tract distally, is a ciliated gutter which is confluent with the narrow

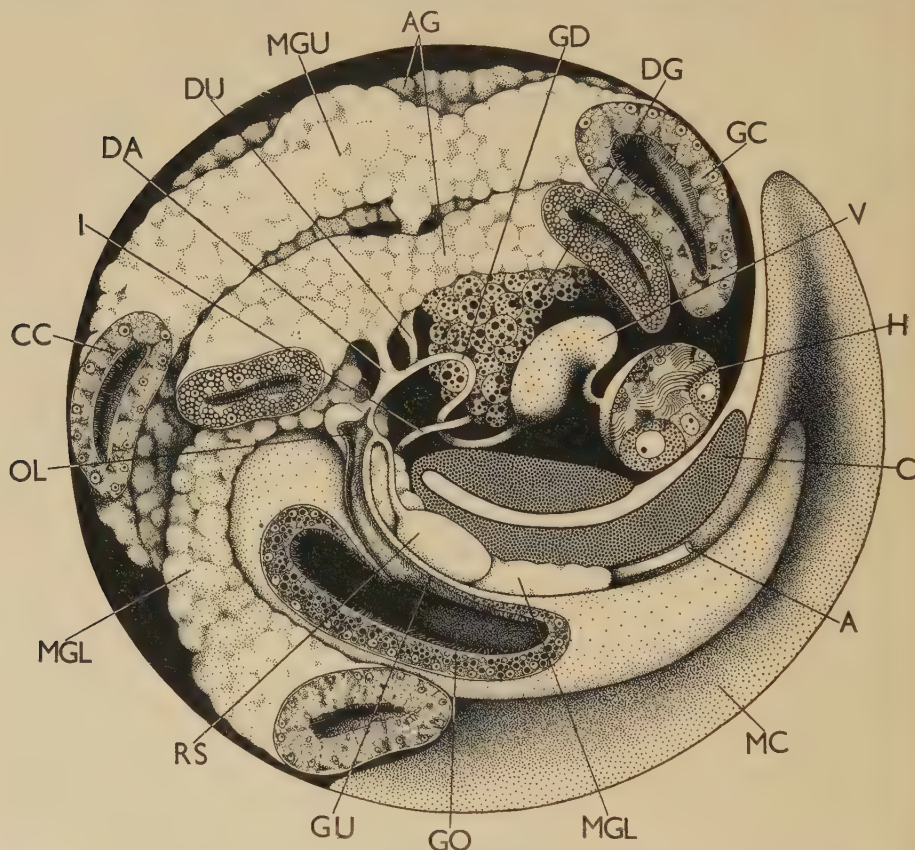


Fig. 11. *Odostomia lukisii*. Stereogram to show the disposition of the reproductive organs. The visceral hump has been cut across at the level of the reproductive ducts and the cut surface is viewed from above; the haemocoel is black. $\times 104$. A, anus; AG, albumen gland; C, columellar muscle; CC, ciliated cell; DA, duct of albumen gland; DG, digestive gland; DU, duct of upper mucous gland; GC, gland cell; GD, gonadal duct; GO, glandular part of pallial hermaphrodite duct; GU, gutter along GO; H, hermaphrodite gland; I, intestine; MC, mantle cavity; MGL, lower mucous gland; MGU, upper mucous gland; OL, opening of lower mucous gland into pallial hermaphrodite duct; RS, receptaculum seminis; V, seminal vesicle.

hermaphrodite duct (GU). Initially this channel communicates with a globular receptaculum seminis (RS) in which unorientated sperm are always to be found. An excess of spermatozoa may surround the entrance to the duct of the receptaculum and extend in all directions from there. The gland cells of the

pallial duct are the first to differentiate and to become functional: during early sexual activity, when only the male system is mature, the cells are distended with large secretory spherules of a protein nature. Later, during a period of egg laying, the appearance of the cells suggests that they are inert—reduced in size, with less abundant and smaller spherules which stain not uniformly, but in varying degrees of intensity, with both iron haematoxylin and azan. This gland is, therefore, assumed to be a prostate, and it is uncertain whether it has any function during the female phase.

The outstanding characteristic of the reproductive system of the pyramidellids is the position of the penis: in no other family does any structure except the digestive tube and its intrinsic glands and muscles pass through the nerve ring. In the pyramidellids, however, this position is also occupied by the penis (Fig. 1). The penis is invaginable and completely concealed except during copulation, when, as a long whip-like structure, turgid with blood and tapering to a fine point, it is passed into the mantle cavity and through the genital aperture of the partner. The penis retracts into a tubular sheath (PSS), within which it lies freely, like a partly invaginated finger of a glove, with its tip at some distance from the external aperture (PO). The sheath lies in the haemocoel dorsal to the gut and may be flung into one or two broad loops when the animal is withdrawn into its shell. The walls of the penis and its sheath are continuous and retraction is brought about by their intrinsic muscles (Fig. 12, CM, LM) and the consequent expulsion of blood into the general haemocoel. These muscles resemble those of the buccal pump in that the fibrillae are striated. Opening into the dorsal wall of the penial sheath in front of the tip of the retracted penis is the short, wide duct of a large, muscular sac which lies immediately within the body wall (Fig. 1, SS). The sac and its duct are ciliated, the cilia exceeding five times the height of the cells in length. An epithelium with long, closely set cilia also lines the anterior part of the sheath to the external opening (PO). Elsewhere the epithelium of the sheath, and also that of the penis, are cuticularized. A second duct, the vas deferens, arises from the muscular sac closely behind the first and runs in the thickness of the dorsal wall of the sheath (Fig. 12, VD) towards the base of the penis into which it passes (VD 1), to open at the tip. It is not ciliated, but its walls are muscular. The path of the spermatozoa from the common genital aperture can thus be followed along the seminal groove through the anterior ciliated part of the penial sheath into the sperm sac and thence to the tip of the penis along the vas deferens.

During copulation the individual which acts as male creeps on to the dorsal surface of the shell of its partner, everts the penis and bends it ventrally to reach the mantle cavity of the female. Animals which have been separated during copulation, fixed and sectioned, show, at least as far as that acting as female is concerned, spermatozoa filling the receptaculum, surrounding the opening of its duct into the pallial oviduct and concentrated along the ciliated gutter which connects the opening with the genital aperture. Perhaps the penis

discharges the spermatozoa into the ventral gutter and then they make their own way to the receptaculum. In the animal acting as male only a few sperm are found in the sperm sac, which is probably merely a temporary storage place for them before they enter the penis. As in *Omalogyra* (Fretter, 1948), the sperm must have been transferred to this sac prior to copulation, for it is difficult to see how they could get there after the penis has been everted.

The egg masses of *Odostomia* spp. are laid in irregularly shaped heaps in the vicinity of the animals upon which they feed. The spawn of *O. rissoides* is described by Pelseneër (1914) and a later account is given by Rasmussen

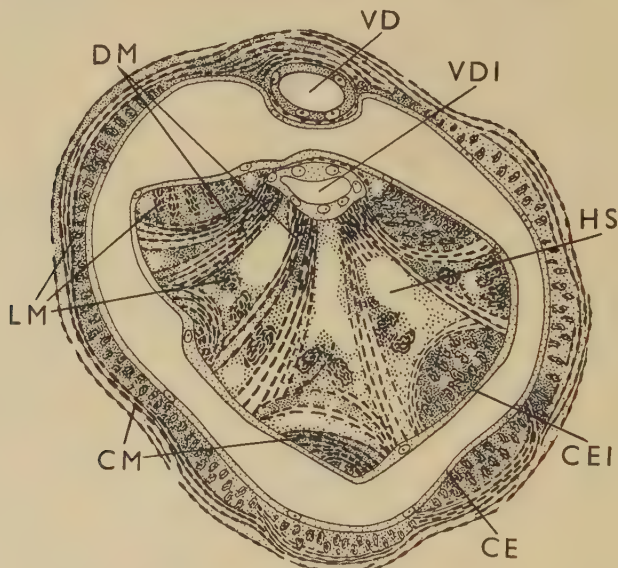


Fig. 12. *Odostomia*. Transverse section of penis in sheath. $\times 600$. CE, epithelium of penial sheath; CEI, epithelium of penis; CM, circular muscles; DM, dilator muscles; HS, blood spaces; LM, longitudinal muscles; VD, vas deferens in penial sheath; VDI, vas deferens in penis.

(1944), who shows that each egg is surrounded by a layer of granular albumen which is, in turn, encased in a mucous envelope or capsule. Between one egg and the next the mucous layer narrows to a fine strand. In this way all the eggs in a mass, which, according to Rasmussen (1944), may amount to five hundred, are linked into a continuous chain and then are still further surrounded and cemented together by a second and more plentiful layer of mucus, the outermost covering of the spawn, by means of which it is fixed to the substratum. An examination of the egg masses of *O. plicata* and *O. eulimoides* shows that they have a similar construction; thus they agree in general plan with those of the opisthobranch *Onchidella celtica* (Fretter, 1943). The staining reactions of the secretions which surround the eggs suggest the origin of these from the three glands attached to the hermaphrodite duct—the albumen gland and the

upper and lower mucous glands—and the relative size of these is indicative of the volume of secretion produced by each in a single egg mass. The lower and larger mucous gland supplies the ample outer jelly and the upper one the capsule wall which encloses each egg with its supply of albumen and separates it from its neighbours.

The eggs are presumably fertilized in the upper part of the genital duct where sperm abound after an egg mass has been deposited, many of these superfluous spermatozoa becoming entangled in the egg coverings. The developing veliger gradually uses up the albumen as food, and in *Odostomia eulimoides* its development to a free larval stage, when kept at a temperature of about 18° C., may be completed within 10–12 days.

Lebour (1932) describes the free veliger of this species with its mobile, bilobed velum, eyes far apart, the transparency of the tissues displaying the relatively large stomach, long intestine and bilobed digestive gland. The general arrangement conforms with that of a typical gastropod veliger, for as yet no adult specialization is apparent; these first appear in the buccal and oesophageal regions of the late veliger. Lebour (1932) suggests that the larval life is short; this suggestion is supported by Thorson (1946) and has now been confirmed by actual observation: the free-swimming larval life lasts from 3 to 4 days, the larvae then becoming benthic and the metamorphosis of the gut rapidly achieved. In the metamorphosing larva the long introvert with its papillated surface, the stylet, the buccal pump and the large salivary glands may all be distinguished, and during further growth the intestine becomes relatively shorter, whilst the stomach is incorporated into the digestive gland. The eyes are now close together as in the adult. The penis, however, is not yet developed, so that the gut is the only tube passing through the nerve ring.

The eggs of *O. plicata* can be distinguished from those of *O. eulimoides* by their yellow pigmentation. They are laid in crevices of stones or rocks where the adults live. The veliger is freed from the capsule in about a fortnight and its structure agrees with that of *O. eulimoides* and *O. rissoides* (Rasmussen, 1944). Thorson (1946) suggests that according to the appearance of the larval shell the free veliger life of this species is longer than that of *O. eulimoides*, but the exact time has not been estimated.

THE PROCESS OF FEEDING

The process of feeding has been watched in several species of *Odostomia*—*O. lukisii*, *O. unidentata*, *O. scalaris*—as well as in *Chrysallida spiralis*, and as the structure of the gut appears to show very little variation throughout the family Pyramidellidae it is probable that the process is similar in all species.

Chrysallida spiralis may be found sitting on the sandy tubes which are inhabited by the polychaete worm *Sabellaria*. When not feeding the mollusc will lurk in any little hollows in the irregular sandy mass which colonies of this

worm manufacture, but when they desire to feed they perch themselves close to the opening through which the head of the worm will protrude. For long periods of time they may be seen sitting in this position, the head and foot out of the shell, the tentacles held upwards and forwards, facing the opening of the worm's tube. Currents produced by the cilia on these bring water streaming to the head of the mollusc from the region of the opening in the tube and it is probable that the mollusc is in this way made aware not only of the presence of a tube, but of the extension or otherwise of the worm that dwells within. When the polychaete cautiously emerges from its tube, however, and starts spreading its tentacles over the surroundings in order to pick up food particles then the mollusc may also start to feed: the proboscis is everted, gradually rolling outwards from the mouth till it forms a long narrow cylinder tapering gently to the sucker at its tip. The basal covering, near the tentacles, tends to be smooth, whereas nearer the sucker the peculiar papillae that lie in the epithelium give it a villous appearance. The whole proboscis can be gently waved about in the water, and the mollusc moves it slowly and delicately up to the neighbourhood of the tentacles of the worm, until actual contact is achieved. This is obviously made as quietly as may be, but the first time that it occurs the worm will usually jerk slightly, though it will not withdraw completely into its tube. The proboscis insinuates itself gently between the tentacles until it lies on their median face; there, still elongating, it slides down the ciliated groove that runs along a tentacle towards the mouth, into which its tip disappears. At this stage the proboscis is enormously elongated and as it is almost transparent the whole of the anterior end of the alimentary canal may be seen lying within. The oral tube, buccal pump and salivary glands occupy the distal half or thereabouts and from them the oesophagus runs as a narrow tube through the basal part of the proboscis until it disappears out of sight into the denser tissue of the main part of the body of the mollusc. As the buccal pump can be seen working and waves of peristalsis passing along the gut it is clear that the mollusc is sucking food into the alimentary canal, but as the tip of the proboscis is invisible, hidden inside the gut of the polychaete, it still remains uncertain what the source of the food may be and, of more interest, what exactly the stylet is doing during the process.

This, however, may be made out with certainty if other pyramidellids, like *Odostomia lukisii* or *O. unidentata* be examined. Both of these species are to be found on stones on which the tubicolous polychaete worm *Pomatoceros* is living, and they may be found lurking at the mouth of the tubes of these just as *Chrysallida spiralis* does near the mouth of *Sabellaria* tubes. When a *Pomatoceros* has expanded its crown of branchial filaments it may be observed that a nearby *Odostomia* will then project its proboscis towards the worm. As the proboscis moves nearer the worm it often rotates in a spiral as if it were carrying out exploratory movements, and, as before, the final approach to the filament of the worm is made apparently with as great delicacy as possible

so as to disturb the prey as little as may be. When it is recalled that these delicate movements are carried out by a proboscis that extends to a length many times that of the rest of the animal the efficiency of the muscular control will be realized. On first contact the polychaete may jerk its crown of filaments away from the proboscis, or even withdraw into its tube altogether, and if this movement on its part is at all sudden a corresponding partial or total withdrawal of the proboscis of the mollusc will take place. Sooner or later, however, the proboscis will be extended once more, and it has been noted on several occasions with what remarkable accuracy the proboscis will reach out to the exact spot with which contact with the filament was previously made, as if the mollusc had some exact kind of kinaesthetic 'memory'. When contact is finally permitted by the worm the sucker at the tip of the proboscis of the mollusc is slid gently along the tentacle until, presumably, a suitable spot is found, usually on the outer side of the filament. Then suddenly the sucker grips the epithelium of the filament, and the stylet may be seen to drive outwards so that it is clearly being used to perforate the body of the worm. Vigorous pumping movements of the buccal apparatus may then be seen and it is obvious that fluid, blood and, perhaps, cells loosened from the worm are being sucked into the gut of the pyramidellid. The polychaete clearly feels the movements of the proboscis and the stabbing of the stylet in most cases, but worms have been observed which allowed the proboscis to move amongst the branchial crown and to slide up and down the filaments and feed in this way without any very pronounced reaction, though it must be remembered that the mollusc always appears to perform these movements with the very greatest caution.

The grip which the pyramidellid obtains on its prey is fairly secure; at least moderate movements of the branchial crown of the polychaete do not dislodge the sucker: it requires a sudden withdrawal to effect this, though we have not been able to avoid the conclusion that the mollusc then lets go, as if to avoid any danger of the proboscis being pulled into the tube and trapped or damaged in any way.

As the differences which have been found to exist between the alimentary canals of the various pyramidellids are confined to apparently unimportant details it would seem that all these animals feed in the same general sort of way.

DISCUSSION

Apart from a few instances the Pyramidellidae are a group of gastropods little mentioned in the literature of malacology, though what has been said has tantalizingly indicated that the group would be of extreme interest were more known about its ways of life. Thus the work of Jeffreys (1867), Pelseneer (1914) and Rasmussen (1944) had suggested that the animals are epizoidic in their habit, without making it completely clear whether their association with other animals was confined to using their shell as a home, or to picking up, using their proboscis as a pipette, mucus and other secretions from the body of the animal on

which they lived, or whether they were indeed true ectoparasites and fed on the body of a host. That some such idea was in the minds of most malacologists is probable, since the Pyramidellidae were associated by Thiele (1929) with the families Melanellidae (= Eulimidae), Stiliferidae and Entoconchidae in the stirps Aglossa, all these families containing animals known to be parasitic in their mode of life. Winckworth (1932), too, places these families side by side, although he refrains from uniting them more closely by avoiding all grouping within the order Mesogastropoda.

The description which has been given above, however, makes it quite plain that the pyramidellids are ectoparasites, and that they live on the blood and perhaps tissue débris of other animals on which, or in the neighbourhood of which, the mollusc passes the greater part of its life. Each species of pyramidellid appears to be associated with one definite host, and as might be expected these are, so far as is known, sessile organisms which are easily found, and which must, if they are to survive at all, from time to time protrude some part of their body for the collection of food, and so make it available simultaneously to the gastropod. The list of hosts which has so far been gathered definitely is:

<i>Chrysallida spiralis</i>	...	<i>Sabellaria</i> spp.
<i>Odostomia unidentata</i>	...	<i>Pomatoceros triqueter</i>
<i>O. lukisii</i>	...	<i>Pomatoceros triqueter</i>
<i>O. scalaris</i>	...	<i>Mytilus edulis</i> (small only)
<i>O. eulimoides</i>	...	<i>Pecten maximus</i> and <i>Chlamys opercularis</i>
<i>O. trifida</i>	...	<i>Mya arenaria</i>
<i>Turbonilla jeffreysii</i>	...	some coelenterate, probably <i>Halecium</i> sp.

These species of pyramidellid will be found, with surprising abundance, as they are not really uncommon animals, in the vicinity of the particular host upon which they feed. They will be found to feed on no other animal. At Plymouth, *Turbonilla jeffreysii* may be dredged from the localities where the hydroid *Halecium* abounds, and that the mollusc is in fact feeding upon it is suggested by the occurrence of masses of nematocysts in the cells of the innermost part of the oesophageal epithelium, which are similar in size to those in the cells of the hydroid. Actual feeding has not, however, been observed in this species. Another species of *Odostomia*, *O. plicata*, is to be found in association with *Pomatoceros*, occurring, in the Plymouth district, at a lower level on the beach than *Odostomia unidentata* and *O. lukisii*. It feeds less willingly when kept in captivity and thrusts its proboscis out at a variety of creatures—even on to the antennae of living amphipods. On two occasions sponge spicules have been found in its gut, suggesting that this species may suck the tissues of a sponge. Although the nature of the mode of life of pyramidellids has been verified for a mere handful of the forty-odd species listed by Winckworth (1932), the gut is of such homogenous structure in all the species that have been investigated, that there is little doubt that they all live in the same general

fashion and that further work will lead to the discovery of the correct host for each species. Until this is known no search for a given kind of pyramidellid can be productive, and the old records of habitat given by Jeffreys (1867) or Forbes & Hanley (1853), such as 'under stones', 'on corallines in rock pools', etc., are valueless as indications as to where the animals really live. When the host is known success in collecting can usually be relied upon.

There are a few clues in the literature regarding hosts of some of the species for which they are not yet known: Marshall (1900) notes the occurrence of *Turbonilla rufescens* on 'the leathery tube of a sessile annelid' and of 'dwarf specimens of *Odostomia albella* with littorinae'. Gardiner (1934) mentions the occurrence of *O. perezii* Dautzenberg and Fischer with *Phascolion strombi*.

The alimentary canal of the various pyramidellids which have been examined varies from species to species only in the very slightest way: the stylet is short in some (*Odostomia eulimoides*), longer in others; there is a separate stylet tube and oral tube in *Chrysallida* and *Odostomia*, whereas in *Turbonilla* there is but the one tube along the centre of which the stylet runs; the papillation of the introvert is pronounced in *Odostomia unidentata* and *O. plicata*, less so in *O. lukisii* and *Chrysallida spiralis*, and is hardly indicated in *Turbonilla*; the salivary glands are better developed in *T. jeffreysii* than in the other genera—perhaps in connexion with the habit of that species of feeding on coelenterates, where a copious salivary secretion might have a special significance in desensitizing the nematocysts (Pantin, 1942). Apart from these relatively unimportant details the gut is very similar throughout the family, and the interest in it lies, not in the variation from species to species, but in trying to homologize the very specialized arrangement found here with the more typical gastropod plan. Practically all the specialization lies in the anterior end of the gut. From the region of the buccal pump onwards the general plan of the gut does not depart significantly from what might be expected—an oesophagus runs back to a stomach and from there an intestine passes to the mantle cavity. The stomach is extremely simple, and is clearly just a place where oesophagus, digestive gland and intestine join, but that is no more than might be expected in animals of such small size feeding on a simple diet (see Fretter, 1948).

The main interest centres in the homologies of the anterior region and two structures may be used as guides to the correct interpretation of these: the salivary ducts and the labial ganglia. In the typical gastropod mollusc the mouth opens by a short oral tube into the buccal cavity. On the floor of the buccal cavity is placed the odontophore and along its roof runs the anterior end of the dorsal food channel, separated from the more lateral portions of the cavity by extensions of the dorsal folds. External to the roof of the cavity lie the salivary glands. Their ducts run in connective tissue, one at the base of each dorsal fold, and open into the buccal cavity dorsolaterally, near its anterior end, about the level at which the dorsal folds end. Anterior to this part the roof of the buccal cavity slopes ventrally into the dorsal wall of the oral tube and it is

in this region that a jaw, or jaws, will be developed, should the animal possess such structures. These arise as cuticular growths from the epithelium covering the dorsolateral wall of the buccal cavity and oral tube. Often the lateral parts, and, always, the anterior end of the jaws are lifted off the epithelium upon which they have been produced so that they project freely into the buccal cavity anterior to the apertures of the salivary ducts. Now, were the two salivary ducts to run together so as to open into the roof of the buccal cavity on a median papilla and were this then to elongate and grow forwards, it would rapidly reach the level of the jaws, and if the free edges of these structures were further supposed to grow ventrally around the salivary duct in its new position a chitinous tube would have been produced, attached dorsolaterally to the epithelium of the buccal cavity at its inner end, but free anteriorly, and this would surround a tube formed from the fusion of the two ducts of the salivary glands. In other words, the condition exhibited by the pyramidellids would have been attained. That the cuticular stylet is, indeed, dorsal, is further shown by the position of the labial ganglia, which lie on the opposite side of the oral tube at the level of the mouth, and by the buccal ganglia which are likewise placed ventral to the apparatus. These relations by themselves would indicate that nothing in the present arrangement could correspond to a radula, a structure which normally lies ventral to the buccal commissure. The glands lying in the oral tube and buccal cavity in the pyramidellids would correspond to the mucous glands which lie scattered over the buccal cavity of other gastropods, more especially in its dorsal part. Nothing comparable to dorsal folds or dorsal food channel seems to occur in the pyramidellids, however: the innermost part of the buccal cavity seems to have become specialized along completely different lines to produce the buccal bulb, whilst the oesophagus is a simple, elongated crop-like structure without any of the characteristic glandular areas of the typical prosobranch.

In *Turbonilla* a single aperture on the sucker leads into a simple oral tube in which the stylet lies (Fig. 5); in *Chrysallida* and *Odostomia* (Figs. 1, 3 and 4) the sucker has a ventral mouth and a dorsal stylet aperture, and two tubes lie parallel to one another in this portion of the gut. How may these have arisen? The probable explanation is to be seen in the occurrence, in a gastropod like *Patella*, of a pair of inner lips (Graham, 1932, Fig. 1). These are attached to the lateral walls of the oral tube, ventral to the jaws, and they may be moved across the oral tube from side to mid-line so as to act like a curtain, dividing the tube into a dorsal half into which the jaw projects, and a ventral half which would be separated from the part in which the jaws lay. Were this contiguity to become a fusion, and were the base of the jaws to abut on, or fuse to, the base of the fold, then precisely the situation which is exhibited in *Chrysallida* and *Odostomia* would have arisen. In this way stylet aperture and apparent mouth may be shown to be merely parts of the original mouth, and the stylet tube a separated portion of the original oral tube.

The evolution of a long proboscis is clearly a necessary feature in the particular feeding habits that the pyramidellids have adopted, and this has apparently involved the penis as well, so as to give rise to the peculiar arrangement by which the sheath of that organ lies within the nerve ring ventral to the oesophagus. In the typical gastropod the mouth lies ventral to the tentacles and the penis is placed on the right-hand side of the head behind and below the right tentacle. An acrembolic proboscis is produced by an elongation of the tip of the snout, anterior to the tentacles, so that the mouth comes to be placed at the summit of a long pretentacular extension, which is everted and appears as such only when the creature is feeding. At other times it is withdrawn and a 'mouth'—though not the true mouth—lies in the usual position. Now suppose that the elongation occurs behind the penis: that will then lie near the tip of the proboscis when elongated and would be carried into the introvert when the proboscis was withdrawn, and the ciliated groove running along the right side of the head from the genital opening to the penis would appear to end at the mouth of the introvert. This consequence of the production in this particular way of a long proboscis produces unnecessary complexities in the functioning of the reproductive apparatus, and it would be needful to suppose that the penis, now brought far inside the body by its association with the introvert, has gradually separated itself from the introvert, and that its external opening has migrated forwards along the ventral wall of the introvert until it finally reached the surface of the body once again. This migration forwards of the opening of the penis gives rise to a long tube, the penial sheath, which, as it has been formed by separation from the introvert, must penetrate the nerve ring, and which will open to the exterior near the mouth. The mentum must have arisen after this migration has taken place, since it separates mouth and penial opening, and it is, therefore, a novel structure without any deeper significance, perhaps, than a barrier between these two apertures. It is tempting to think that the original cephalic tentacles of the ancestral pyramidellid were also involved in the formation of the introvert and have been lost and replaced by new structures, which would explain the peculiar shape of these and the fact that the eyes lie on their inner instead of their outer sides. But this position may merely be the result of a direct migration such as occurs during development (Lebour, 1932).

The bulk of the digestive processes appear to go on inside the digestive gland, the oesophagus acting primarily as a crop. Whether the peculiar lining of the introvert has any digestive significance or not we are unable to say, but it is interesting to note that various particles of detritus, diatoms and such like, are sometimes to be found inside the retracted introvert: this is probably merely accidental contamination in view of the fact that its surface is probably sticky from the secretion of the numerous glands placed there. The precise function of these remains obscure. As they are most abundant in the neighbourhood of the sucker and least near the base of the proboscis it would seem likely that

they are concerned with the process of feeding, as it is precisely the part of the proboscis which comes most into contact with the body of the prey which carries the greatest number of glands. They therefore most probably lubricate the movement of the proboscis so as to make it less likely of notice by the prey.

The second main point to which attention must be directed is the systematic position of the family Pyramidellidae. Although from the time of Mørch (1865) suggestions have been put forward that the family, if not actually opisthobranch, may be the group of prosobranchs from which the opisthobranchs originated, they have always in fact been classified as prosobranchs, usually associated with other groups of known or suspected similar feeding habits—explicitly or implicitly in an aglossan grouping. It is true that the pyramidellids resemble, for example, the Eulimidae and Stiliferidae in having lost the radula, but the most cursory examination of a eulimid (our own unpublished observations) or stiliferid (Kœhler & Vaney, 1908) shows that otherwise there are few points of agreement between the two families. The Eulimidae and the Stiliferidae are certainly extremely specialized in connexion with their ectoparasitic habit, but this has taken place along completely different lines from the Pyramidellidae.

The question as to the true systematic position of this family has lately been raised again by Thorson (1946), who points out that the characteristically heterostrophic larval shell of the pyramidellids is a feature which they share with a large number of opisthobranchs. On the basis of the work described in the preceding pages a comparison of pyramidellids and other gastropods may now be extended to other systems and the classification of the family reviewed in the light of the results of this.

In so far as the pyramidellids have a spirally coiled calcareous shell into which the entire body is retractile, a foot bearing an operculum, and a large anteriorly directed mantle cavity they resemble the prosobranchs. The same holds for the occurrence of a long proboscis. But when these things have been pointed out then almost all the specifically prosobranch characteristics of the animals have been mentioned. The various other ways in which the body of a pyramidellid differs from that of a typical prosobranch may be due (a) to specialization in connexion with its ectoparasitic life, or (b) to the fact that it is small and may therefore be secondarily simplified, or (c) to the fact that it is really an opisthobranch. In relation to the third possibility it is well to recollect that opisthobranchs like *Actaeon* may have spirally wound calcareous shells into which the body may be withdrawn and which can be closed by an operculum, and that they may have an anteriorly directed mantle cavity and be streptoneurous, so that the fact that the pyramidellids have the characteristically prosobranch features enumerated above does not debar them from being opisthobranchs.

So far as external features are concerned the contents of the mantle cavity first call for attention. Here no ctenidium is developed: this may be due to

small size, as in *Omalogyra* (Fretter, 1948), but it is noteworthy that in the family Actaeonidae the gill is reduced to a single triangular leaflet, whilst the main current of water is maintained within the mantle cavity by strips of ciliated epithelium as in *Odostomia*. As Fretter (1948) has suggested, in connexion with another group of gastropods, the forward projection of the kidney into the mantle may be valuable for the sake of the capillary bed which migrates with it: this feature also occurs in pyramidellids and in *Actaeon*. In another family of opisthobranchs, too, the Diaphanidae, the mantle resembles that of the Pyramidellidae in containing a dark brown-red gland of unknown significance. The mantle edge on the right side has a small lobe-like projection in pyramidellids: the actaeonids and hydatinids amongst the opisthobranchs have a similar process, although it is there larger and glandular. The tentacles carried on the head of a pyramidellid are ear-shaped: those on the head of the opisthobranchiate Hydatinidae are similar; the eyes are placed on their median sides on both groups, and in many other opisthobranchs that is also the position in which they are found, although there they are often sunk below the surface, a tendency not noticeable in the pyramidellids, unless convergence towards the mid-line is the first stage towards such a position.

In the construction of the alimentary canal there are several points in which pyramidellids and opisthobranchs agree: the complete suppression of the oesophageal glands and dorsal food channel (Graham, 1939); the tendency for the oesophagus to form a crop-like expansion and for the stomach to be merely a space into which the ducts of the digestive gland discharge (Graham, 1949); the shortness of the intestine; the tendency for the digestive cells of the digestive gland to become laden with spherules (Fretter, 1939)—all these are characteristics of opisthobranchs in general. There are one or two points in which the pyramidellids show similarity to special groups of the opisthobranchs and these groups are, as observed in the discussion of the external features, the most primitive families. In the hydatinids, for example, Thiele (1931) notes that the oral tube is very long, and it is well known that in the Actaeonidae the radula carries only extremely small and weak teeth, a characteristic also encountered in other groups of primitive tectibranchs. In other points the anatomy of the pyramidellid alimentary canal is much specialized, as is only to be expected in view of the parasitic mode of life which the group has adopted, but even here it may be noted that the buccal pump may be paralleled in the ascoglossans (Fretter, 1940).

It is rather difficult to use the nervous system of the Pyramidellidae as a clue to the relationship of the family, as it is possible for prosobranchs to be euthyneurous and for opisthobranchs to be streptoneurous. Of greater importance, perhaps, is the degree of concentration of the ganglia towards the formation of a nerve ring, and in this connexion the pyramidellids show a clear trend towards the opisthobranchiate condition. Pelseneer (1899) attempted to refute Mörch's original suggestion that the Pyramidellidae were opistho-

branches on the grounds that the cerebral ganglia, like the pedal, were so close together that they were practically fused with one another, that the nerve ring was not anterior to the salivary glands and that the statocyst contained only one statolith—all points on which they differed from the 'Bulléens'. The first of these characteristics, however, is by no means unknown in the Opisthobranchia, while the second may very well have arisen in relation to the extreme specialization which the anterior end of the gut has undergone.

Further evidence bearing on the relationships of the family is provided by the reproductive system, and in this, as in the alimentary system, there are several points in respect of which pyramidellids resemble opisthobranchs rather than prosobranchs: the gonad is hermaphrodite, not unisexual; the ova receive their albuminous covering as they pass along the sperm-oviduct and do not enter the albumen gland (Fretter, 1946); large mucous glands provide a jelly which forms the outer, protective covering of the egg mass and there is neither capsule wall nor pedal gland to mould it; an open seminal grove leads from the common genital aperture to the penis, which is invaginable; a sperm sac is attached to the penial sheath and is filled with spermatozoa before each copulation; the veliger has a sinistral shell. The closest agreement is with the more primitive families of the tectibranchs, in which the genital duct is monaulic and male and female apertures lie at some distance from each other. Except for minor variations in proportion the penis and its sheath agree in general plan and in histology with those of *Philine aperta* (Pruvot-Fol, 1930): when the penis is extended a flow of sperm into it is rendered impossible by the arrangement of the ducts and a reservoir or sperm sac is therefore required.

Finally, it is to be noted from the conchological side, that the tooth on the columella—from the presence of which the genus *Odostomia* acquires its name—so characteristic of the Pyramidellidae, is also to be met with in the Actaeonidae, Ringiculidae and Diaphanidae amongst the tectibranchs.

If all these points be taken into consideration there is such a large number of characters in which the resemblance between the family Pyramidellidae and the Opisthobranchia is marked that it seems logical to remove the family from the subclass Prosobranchia to the subclass Opisthobranchia.¹ As to the precise position within the Opisthobranchia that the Pyramidellidae should occupy there is some doubt, because of our lack of knowledge of the soft parts of such opisthobranchs as *Actaeon*, *Hydatina*, *Diaphana* and *Haminea*, and, until such animals have been properly investigated, any assignation of the Pyramidellidae to a definite position must be tentative. In view of their stout, spiral shell and operculum, however, they are more primitive than all the opisthobranchiate families other than the Actaeonidae; because of their euthyneurous nervous system and loss of ctenidium they are more advanced than

¹ Owing to a misprint we appear (Fretter & Graham, 1949) to have said precisely the reverse of this in a letter to *Nature*.

that family but less than the Diaphanidae. Until more is known of the anatomy of these two families of the opisthobranchs the family Pyramidellidae may be placed between them.

The Pyramidellidae is not the only family of gastropods superficially prosobranch in appearance but probably opisthobranch in reality. The Omalogyridae, in which *Omalogyra* has been recently described (Fretter, 1948)—and from a preliminary study *Ammonicera* would seem to agree—have also an imposing assemblage of characters in common with the opisthobranchs: the animals are hermaphrodite; the penis is a long, whip-like muscular tube into which, during copulation, sperm are passed from a sac; there are no oesophageal glands; the stomach is simplified and is merely a space within the digestive gland; the intestine is short; large and histologically complex glands open into the mantle cavity, which is without a ctenidium but has strips of ciliated epithelium running forwards from the anus to maintain an exhalant flow of water. Unlike the opisthobranchs, but like most prosobranchs, the Omalogyridae produce egg capsules. It is uncertain to which group of the opisthobranchs these minute gastropods should be allied, for our present knowledge of the opisthobranchs is particularly poor so far as the most primitive members of the subclass are concerned—and these are the very ones involved.

SUMMARY

The family Pyramidellidae contains a number of species of gastropod molluscs of similar structure and mode of life.

The shell is calcareous and spirally wound and may be closed by an operculum. The foot bears a transverse fold anteriorly, the mentum (Fig. 1, MT), separating the opening of the penial sheath (PO) below from the mouth (M) above. It has a lateral glandular streak on each side (Fig. 2), presumably sensory.

The head has ear-shaped tentacles (Fig. 1, T), richly innervated and with cilia setting up a strong water current, so that they constitute a powerful sensory mechanism. The eyes (E) lie between the tentacles.

The mantle cavity faces anteriorly, is wide and deep. To it open the anus, at its inner end; the kidney, on its roof; and the single genital aperture, on its floor. There is neither ctenidium nor osphradium, but well-developed hypobranchial and other glandular fields. A circulation of water is maintained by strips of ciliated epithelium in relation to these. A special pigmented structure, perhaps glandular, lies by the genital aperture and a ciliated tract leads from there to the opening of the penial sheath.

The 'mouth' leads to a long introvert with a specially glandular papillated epithelium (Fig. 1, EP; Fig. 8, EPL, EPT). At the inner end of this the true mouth (Figs. 1 and 4, M) lies on a sucker (Fig. 4, MCS, MOS) and an elongated oral tube (OT) leads to the buccal cavity. From a dorsal pouch of this (Figs. 1 and 3, DP)

a long stylet projects forwards (s), in a separate tube in *Chrysallida* and *Odostomia* but in the main oral tube in *Turbonilla*, and may be thrust outwards from the sucker. The stylet encloses the common duct of a pair of salivary glands (Fig. 3, USD). The posterior part of the buccal cavity is differentiated into a double muscular sac, the buccal pump (Fig. 1, BP), and the walls of this, the salivary ducts and sucker contain striped muscle fibres. From the buccal pump the oesophagus (o) runs to the stomach and digestive gland and thence a short intestine passes to the anus. There is no radula.

In the vascular system only a posterior aorta leaves the heart. The anterior aorta arises from the visceral haemocoel. Blood cells, active as excretory amoebocytes, are common.

The nervous system (Fig. 10) is mainly concentrated into a ring round the oesophagus and penial sheath and is euthyneurous. An osphradial ganglion (OG) lies in the mantle on the left and two pairs of ganglia lie ventrally in relation to the anterior end of the gut: these are the buccal ganglia (Fig. 1, BG), close to the buccal pump, and the labial ganglia (LC) in relation to the sucker.

The gonad is hermaphrodite (Fig. 11, H) and from it a narrow duct passes towards the mantle cavity (GD), receiving on its way ducts from the albumen gland (AG, DA) and proximal (MGU, DU) and distal (MGL, OL) mucous glands. Opposite the opening of the latter arises the duct of the receptaculum seminis (RS). The initial part of the broad pallial duct is glandular (GO) and is probably a prostate. From the common genital aperture in the mantle cavity an open seminal groove leads to the invaginable penis (Fig. 1, PO). A sperm sac is attached to the penial sheath (ss) and is filled before each copulation.

The eggs, each surrounded by albumen and enclosed in a mucous sheath which is continuous from one egg to the next, are embedded in secretion from the distal mucous gland and deposited in irregularly shaped clumps near the feeding grounds of the adult. The veliger is characterized by the sinistral shell and the pigmented gland on the right side of the mantle. Its oesophagus, intestine and commodious stomach, into which opens the bilobed digestive gland, are greatly modified during metamorphosis at the end of pelagic larval life.

Pyramidellids are ectoparasites. Each species feeds on a particular species of host, usually a tubicolous polychaete or a lamellibranch mollusc, obtaining attachment to the body by means of the oral sucker, piercing the body wall with the buccal stylet and sucking blood, and perhaps tissue debris, by means of the buccal pump.

A consideration of the structure and reproductive habits of the group leads to the conclusion that they are opisthobranchiate gastropods.

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MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1948-49

The Council has to record with deep regret the deaths of Professor Sir D'Arcy Wentworth Thompson, F.R.S., one of the first members of the Association and for many years a member of the Council; of Prof. Johan Hjort, For.Mem.R.S., an Honorary Member of the Association; of Mr R. Elmhirst, Director of the Millport Marine Station of the Scottish Marine Biological Association; and of Prof. Walter Garstang, a former member of the scientific staff and later Vice-President and an Honorary member of the Association.

The following have been elected Vice-Presidents of the Association during the year: G. P. Bidder, Sc.D.; W. T. Calman, C.B., D.Sc., F.R.S.; Vice-Admiral Sir John A. Edgell, K.B.E., C.B., F.R.S.; Prof. A. V. Hill, C.H., O.B.E., Sc.D., F.R.S.; H. G. Maurice, C.B.; E. S. Russell, O.B.E., D.Sc.; Sir Edward J. Salisbury, Kt., C.B.E., D.Sc., Sec.R.S.; Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O.

The Council and Officers

Four ordinary meetings of the Council were held during the year, two in the rooms of the Royal Society, one in the rooms of the Linnean Society, and one at the Plymouth laboratory. At these the average attendance was 16. The Association is indebted to the Councils of the Royal Society and of the Linnean Society for the use of their rooms.

Mr Alfred R. Wagg has been appointed an Annual Governor representing the Fishmongers' Company in place of Mr Benjamin Travers, A.F.C.

In July 1948 Dr G. P. Bidder attended a Royal Garden Party at Buckingham Palace as a representative of the Association.

The Council wish to record their thanks to Dr G. P. Bidder for his generous gift of a portrait of himself painted by the late Mr R. G. Eves, R.A. Dr Bidder made this presentation on the occasion of his fiftieth consecutive year as a member of the Council, and all members of the Association will wish to congratulate him and record their appreciation of his great services over so long a period.

The Plymouth Laboratory

The rebuilding of the east wing of the main building as laboratory accommodation has been completed.

The stainless steel piping in the tank room of the first floor of the main building, which was badly corroded, has been replaced by ebonite piping.

The workshop-store, near the main entrance gates, the limestone walls of which were not weatherproof, has been greatly improved by the construction of cavity walls and has now been rendered completely watertight. At the same time the opportunity has been taken to enlarge the workshop on the upper floor by extending it by 12 ft. to the north. This extension has a concrete floor suitable for carrying heavy machine tools. The cost of the whole of this work has been met from the remaining investments in the Building Fund of the Browne Bequest Fund.

One of the rooms on the ground floor of the north building has been fitted out as a workshop for the physiological laboratory. It has been fully equipped with tools, including a Myford $3\frac{1}{2}$ in. lathe.

The Aquarium

The aquarium has continued to arouse much interest and to attract large numbers of visitors in addition to the frequent attendance of parties of school children under the supervision of their teachers. The health of the fishes and of many invertebrates has been very good, while deaths among the fully established inhabitants of the tanks have been rare. During the year additions have been made to the fishes shown, notably mackerel, red mullet, sea-bream, whiting and John Dory.

Research Ships

The research vessel *Sabella* has worked throughout the year. In November certain alterations and additions were made to her; part of the forward hold was converted into living accommodation for research workers and the bridge was enlarged to accommodate the echo-sounding gear.

The new $61\frac{1}{2}$ ft. motor fishing vessel *Sula* arrived at Plymouth on 21 June 1948. Mr G. A. Steven accompanied her on the trip from Sittingbourne. She was quickly in commission and has proved most efficient and capable of doing all the work required of her in home waters, including hydrographical cruises to mid-Channel.

The *Gammarus* has as usual worked continuously throughout the year.

The Staff

The Council desire to congratulate the Assistant Director, Mr E. Ford, on his appointment as Director of the Millport Marine Biological Laboratory. Mr Ford has been a distinguished member of the laboratory staff since 1913, and he will be much missed at Plymouth. He will be taking up his appointment at Millport on 1 April 1949.

The Council have to report that Mrs E. W. Sexton retired from active work at the Plymouth laboratory on 31 March 1948. Mrs Sexton has been

associated with the laboratory since 1901, for many years as a voluntary worker, and her researches on amphipod crustaceans are of international repute. All will wish her a happy retirement.

Mr D. K. Hill has been appointed to the Staff as Physiologist, in the grade of Senior Scientific Officer; he took up his duties at Plymouth in June 1948.

Mr F. S. Russell attended the eighth General Assembly of the International Union of Geodesy and Geophysics in Oslo in August 1948, as a representative of the International Council for the Exploration of the Sea.

Mr D. P. Wilson and Dr L. H. N. Cooper attended the thirty-sixth meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1948.

Occupation of Tables

The following ninety workers have occupied tables at the Plymouth laboratory during the year:

- B. C. ABBOTT, London (Physiology of dogfish muscle).
- A. A. ALEEM, London (Littoral diatoms).
- FR. AUGSBURGER, Switzerland (Library).
- Dr G. BACCI, Naples (Sex differentiation in *Asterina*).
- Dr E. J. BATHAM, Cambridge (Nerve net of *Metridium*).
- Dr ANNA M. BIDDER, Cambridge (*Sthenoteuthis*, and digestion in *Sepia*).
- Prof. A. A. BOYDEN, New Jersey, U.S.A. (Systematic serology).
- Miss E. M. BROWN, London (Protozoa).
- C. BURDON JONES, Bangor (*Glossobalanus*).
- Dr M. BURTON, British Museum (Nat. Hist.) (Sponges).
- Dr R. W. BUTCHER, Fisheries Laboratory, Nottingham (Marine Flagellates).
- H. W. CHANG, Academia Sinica, Shanghai (Biology of *Callionymus lyra*).
- G. CHAPMAN, London (Mesogloea of *Calliactis*).
- Dr R. I. B. COOPER, Cambridge (Seismic prospecting of sea-bed).
- J. B. COWEY, Cambridge (Basement membrane in Nemertines).
- Dr J. F. DANIELLI, London (Nucleus transplantation in *Echinus* eggs).
- Miss S. DAVIES, British Museum (Nat. Hist.) (Polychaetes).
- Miss E. DRESEL, Cambridge (Excretion in Isopods and Amphipods).
- B. H. DUSSART, Geneva (General).
- P. S. B. DIGBY (Planktonic copepods).
- E. B. EDNEY, Birmingham (Water relations in *Ligia*).
- P. FATT, California (Nerve action potentials in *Sepia* and Selachians).
- J. E. FORREST, London (Nudibranchs).
- H. C. FOUNTAIN, Torpoint (Marine Acarines).
- Dr VERA FRETTER, London (*Proneomenia*).
- M. H. W. GALL, Cambridge (Light penetration in the sea).
- Miss E. GONZALEZ, Manchester (Red Algae).
- A. T. GOODMAN, Plymouth (Library).
- Miss U. M. GRIGG (Biology of Trochids).
- R. E. HALL, Southampton (Marine Chironomids).
- Miss J. HANSON, London (Serpulids and Sabellids).
- Prof. J. E. HARRIS, Bristol (Neurophysiology of dogfish embryos).
- Dr T. J. HART, Discovery Investigations (Ice Diatoms; hake).
- N. I. HENDEY, Admiralty (Hydrogen-ion concentration).

- M. N. HILL, Cambridge (Seismic prospecting of sea bed; and bottom sampling).
 A. R. HOCKLEY, Southampton (Occurrence of *Mytilicola* in *Mytilus*).
 A. L. HODGKIN, Cambridge (Neurophysiology).
 N. A. HOLME (Bottom fauna).
 Dr W. HOLMES, Oxford (Nervous system of *Amphioxus*).
 Prof. SVEN HÖRSTADIUS, Uppsala (Nucleus transplantation in *Echinus* eggs).
 O. D. HUNT, Newton Ferrers (Fouling organisms).
 A. F. HUXLEY, Cambridge (Neurophysiology).
 Dr V. G. JHINGRAM, India (Fisheries).
 Dr B. KATZ, Cambridge (Neurophysiology).
 G. KERKUT, Cambridge (Movement in starfishes).
 R. D. KEYNES, Cambridge (Neurophysiology).
 Prof. W. B. R. KING, Cambridge (Bottom sampling).
 Prof. H. KIRBY, California (Protozoology).
 Dr P. L. KRAMP, Copenhagen (Hydromedusae).
 Dr MARIE V. LEBOUR, Cawsand (Larval Decapods from Bermuda).
 Miss KARIN LINDBLAD, Sweden (Algae).
 Dr I. JOAN LORCH, London (Nucleus transplantation in *Echinus* eggs).
 Dr O. LOWENSTEIN, Glasgow (Electrophysiology of the labyrinth in *Raia*).
 Dr A. G. LOWNDES (Density of aquatic organisms).
 M. D. MENON, Madras (Biology of *Gadus luscus* and *G. minutus*).
 Prof. LILY NEWTON, Aberystwyth (Library).
 W. G. O'DRISCOLL, Admiralty (Hydrogen-ion concentration).
 Dr L. O. OHMAN, Sweden (Physiology of *Echinus* and *Pomatoceros* eggs).
 Dr A. P. ORR, Millport (Research ships).
 Prof. J. H. ORTON, Liverpool (Biology of *Patella*).
 Dr C. F. A. PANTIN, Cambridge (Nerve net of *Metridium*).
 Dr H. E. QUICK, Swansea (Marine Pulmonates).
 Miss M. RIDALL (General biology).
 J. M. RITCHIE, London (Physiology of dogfish muscles).
 T. D. M. ROBERTS, Glasgow (Electrophysiology of the labyrinth in *Raia*).
 Dr D. M. ROSS, London (Facilitation in sea anemones).
 Miss H. G. Q. ROWETT, Plymouth (Library).
 Dr E. S. RUSSELL, Hastings (Decapods).
 G. SESHAPPA, Cullercoats (*Littorina saxatilis*).
 E. W. SIMON, Oxford (Toxicity studies in *Echinus* eggs).
 Miss J. SINGER, Cambridge (*Cordylophora*).
 B. W. SPARROW, Newton Ferrers (Fouling organisms).
 Miss F. A. STANBURY, Plymouth (Library).
 U. STEFANSSON, Reykjavik (Chemistry of sea water).
 Mrs O. TATTERSALL, Cardiff (Mysids).
 J. A. THOMPSON, Cullercoats (Research ships and gear).
 Dr M. A. THYNNE, Plymouth (Microtomy).
 D. W. TUCKER, Liverpool (Ecology of *Patella*).
 Miss VIDYA VATI, Lucknow (Embryology of fishes).
 D. J. VAUX, Lowestoft (Physical oceanography).
 Capt. R. CH. VEEN, Netherlands Indies Government (Research Ships and Hydrography).
 Miss L. E. WAGGE, London (Calcium metabolism in marine animals).
 P. R. WALNE, Conway (Chemistry of sea water).
 Dr C. C. WANG, Academia Sinica, Shanghai (Protozoology).

Dr R. J. WEISS, Luxembourg (General biology).
G. P. WELLS, London (Physiology of *Arenicola*).
Miss E. WHITEHEAD, London (Library).
Miss E. WHITTINGTON, Exeter (Library).
E. J. FERGUSON WOOD, C.S.I.R. Australia (Algae and anti-fouling).
Dr W. H. YUDKIN, Cambridge (Phosphagens in Polychaetes).

A large number of visitors have taken the opportunity of spending a few days in Plymouth to see the work of the laboratory or discuss problems with members of the scientific staff. Among these the following have come from overseas:

Prof. Marcel Avel, Bordeaux; J. J. Baal, Jersey; T. W. Burdon, Fisheries Officer, Malaya; A. B. Cashmore, C.S.I.R., Canberra; Lt.-Cdr. A. P. Cumming, Vice-Consul, Tromsø; Prof. Jan Dembowski, Poland; Dr R. H. Fleming, U.S. Hydrographic Department; J. D. Kelsall, Fisheries Officer, Lake Victoria; Oo King, Burma; Ole Matthiesen, Oslo; Prof. D. Merriman, Director, Bingham Oceanographic Laboratory; R. J. Midwinter, Fisheries Officer, Gambia; R. T. M. Pescott, Director, National Museum of Victoria, Melbourne; H. Postma, Zoological Station, Den Helder, Holland; Dr R. R. Prasad, India; Prof. E. B. Rao, Madras; Prof. J. Runnström, Stockholm; Dr R. Dana Russell, U.S.N. Electronics Laboratory; Prof. Bradley T. Scheer, University of California; Dr Sun Yia-Chu, Director, Geographical Department, Peking University; Cdr. R. H. Thornton, C.S.I.R., Australia; Dr R. Wojtusiak, Poland.

The Easter Vacation Courses were conducted by Mr D. P. Wilson and Mr G. A. Steven, and were attended by forty-four students from the following Universities and University Colleges: Oxford, Cambridge, London, Edinburgh, Glasgow, Liverpool, Birmingham, Bristol, Sheffield, Bangor, Cardiff, Newcastle, Southampton, and from Chelsea Polytechnic and SW. Essex Technical College.

Also during the Easter Vacation Mr A. H. Lewis brought two boys from Wellington College, and Mr A. A. M. Gardiner six from Radley.

At the end of August a course for biology teachers was conducted by Dr J. E. Smith, Dr G. E. Newell and Miss G. C. Evans, at which the attendance, which included some students, was twenty.

Scientific Work of the Plymouth Laboratory Staff

Physics and Chemistry of Sea Water

Dr W. R. G. Atkins continued the recording of daylight during 1947 and 1948 with Miss P. G. Jenkins. The period from 1930 covers thirteen years.

With Dr H. H. Poole and Mr F. J. Warren seasonal changes in the penetration of daylight into the sea were further studied. The cube photometer, with

new rectifier cells, measures the vertical component, downwards and upwards. The visibility of objects viewed against deep water is related to the latter. The horizontal component is measured in four azimuths, and the average angle of obliquity is thus determined. The vertical component was also measured with vacuum cells and colour filters. For some of this work a d.c. amplifier of R.C.A. design was assembled by Mr Warren. In addition to measurements with Dr Poole's original apparatus, some were made with a Tinsley galvanometer on gimbals. Prof. J. H. J. Poole's neon tube photometer, used successfully at sea previously, was combined with an amplifier and counter. Though excellent ashore there is some leakage trouble at sea. A faster rate of flashing—up to 10–12 per sec.—can be measured with the counter than is possible by eye. A simple method has been introduced for determining the extinction coefficient of sea water at moderate depths. Two rectifier photocells, mounted as usual, are connected to a small microammeter so as to oppose each other and their sensitivities are equalized. For the small currents generated when the cells are under opals and green filters the current-illumination relation is rectilinear. The deck cell is then covered by an additional opal which reduces the light to about 65 %, and the sea cell is lowered to balance. A denser opal being substituted, the cell is lowered further and the depth noted again. Finally, both opals are used together, so that the deck cell gives about 6 % of its original current. As always, accuracy depends upon the height of the waves. The microammeter can be held in the hand and is inexpensive. Mr Maurice Gall used an apparatus embodying the same principle on a coastal cruise. It may be termed 'the photoelectric balance by depth method'.

For comparison, extinction coefficients were measured by photoelectric cells and Pulfrich photometer, using the method introduced by Dr Cooper for the latter; though the conditions are fundamentally different it was not expected that the Pulfrich values would be three times as great. The Pulfrich readings altered on standing. It was surprising to see that water from 20 miles out had suspended matter which settled so quickly. The optical examination of sea water was begun to study the effects of light, but is now used to follow the movement and variation of suspended matter and because non-motile organisms suffer vertical movements which alter the light they get. Though the layering, found by Prof. Pettersson in Scandinavian Fjords, is unlikely to be as well marked here, it may be considerably better developed than we thought. Thus for physical and biological reasons it became desirable to study the scattering of a beam of light. Accordingly, a photo-cell was mounted in a tube capable of rotation around a flask and the brilliance of the Tyndall effect was measured at a series of angles, throughout the year, mostly with a selenium cell, but later with a caesium antimony cell and amplifier. For very small currents the Winfield electrometer triode null method is good and was also used to restandardize old photocells and to test new ones.

Dr Atkins and Mr J. M. Ritchie continued the measurement of very low

illuminations using the R.C.A. electron multiplier cell. The use of over 1000 V. in a marine atmosphere entails special precautions. The light of the night sky is detectable over the area covered by a theodolite telescope, and gives a few scale divisions, at the end of nautical twilight (about 80 min. after sunset). This is about 10^{-5} lux, and full sunlight as much as 10^5 lux, so the range of natural illumination measured is of the order of 10^{10} .

During the war Dr Atkins worked on visual range and lamp penetration range for the Air Ministry. He and Dr Poole are trying to apply similar conceptions to under-water visual range. For horizontal visibility a periscope, converted from the drift indicator of a bomber, is used.

Dr Atkins had suggested that autotrophic flagellates might be the major constituent of the phytoplankton, since silicon consumption was inadequate to account for phosphorus taken up were diatoms alone responsible and diatom tests are extremely insoluble. To follow this relation, and gear it to the optical work, he determined the seasonal changes in the phosphate and silicate throughout the water column at E1. The copper cycle was also studied, but for the surface only, since the water-bottles give off copper. To ascertain whether clay in suspension is a source of silicate, with the help of Mr F. A. J. Armstrong, who was appointed an Experimental Officer last spring, a carboy, about 20 l., of water was filtered monthly and the residue analysed after ignition. Inorganic matter—clay and diatom tests—was 12–190 mg. Mr Armstrong's analyses showed that the solids in suspension contained a far greater weight of silica and of iron than was in solution. The aluminium content of the residue decreased greatly in summer, suggesting that an alumino-silicate had gone into solution. It would be well to supplement analyses of nutrients in solution by analyses of suspended matter; for 10 mg. from 20 l. means 0.5 mg./l., or 0.5 g./m.³, or one part in two million, whereas phosphorus, for example, is reckoned in parts per thousand million.

To follow seasonal production of the phytoplankton the deposit on the filter-paper was extracted with acetone. The April extract was a deep yellowish green, but that for August was almost colourless. If the filtration were carried out immediately after collection of the water such extracts could give quantitative results. The extracts now in hand show the general trend well.

Dr H. W. Harvey has continued investigations on the total phosphorus and phosphate in the sea off Plymouth.

The data so far obtained are indicating that the total quantity of phosphorus in the whole water column undergoes no significant seasonal change, although there is some redistribution in depth, the quantity in the upper 20 m. layer becoming somewhat less in summer, with a slight increase in the 20–40 m. layer. Thus, evidence is accruing that the total phosphorus in the water is a distinctive index of different water masses. The quantity in the water off Plymouth fluctuates from month to month, as the water occupying the area moves away to be replaced with water from other areas.

Water masses in the English Channel have been encountered during the course of our ships' cruises, having very different contents of total phosphorus—water columns averaging 11 mg. and others averaging 20 mg. phosphorus per cubic metre.

The increase in dissolved organic phosphorus compounds, which takes place from winter to summer, is presumably an index of the population density of living organisms in the water during this interval; the magnitude of this increase is very different in different water masses. In those with a greater content of total phosphorus more dissolved organic phosphorus had been set free during the first six months of the year, and also, at the time of sampling, there is frequently more plankton present in the water column. With the object of obtaining more data concerning the relation between the momentary plankton population and the total phosphorus content of the water, Dr Harvey has been engaged in developing a meter which registers the water filtered by plankton nets. It is of interest that the eddies or negative pressure set up in the wake of a conical net aid the passage of an unexpectedly large volume of water through the pores of fine-meshed nets.

A method of estimating manganese in solution has been developed and has shown that the sea off Plymouth contains less than 1 mg. soluble Mn per cubic metre, a result in agreement with previous biological estimations. This small quantity is mostly adsorbed on organisms and detritus. In the sea off the Isle of Man more than twice this quantity was found. This is an area where flagellate algae are usually very numerous in summer; these plants have been shown to be particularly sensitive to low concentration of manganese in solution. Various river and lake waters were found to contain 1–40 mg. soluble Mn per cubic metre—considerably more than in the adjacent sea. The results are being published in Vol. xxviii, No. 1 of the *Journal*. Experiments designed to show what happens to dissolved manganese which enters the sea have led to tentative conclusions which it is hoped to develop by the use of radio-active manganese.

During more than half a century a very large mass of physical, chemical and biological records has accumulated from the western English Channel and neighbouring waters. With our present knowledge, particularly of the distribution of nutrient salts and of biological indicators, much of the earlier work now reveals meaning which could not have been seen at the time it was done. Since 1945, Dr L. H. N. Cooper has spent much of his time in an attempt to reassess and correlate the earlier work in the area. At the same time he has been attempting to apply recent developments in the theory of physical oceanography to problems of shelf hydrology. Papers are almost complete on the following: the distribution in the Atlantic in relation to hydrology of the siphonophores, *Muggiaea atlantica* and *M. kochi*, which show much promise as biological indicators, not so much of local water movements as of changes in oceanic circulation; a theoretical method of computing wind-drift of

water with especial reference to an observed change in distribution of *M. atlantica*; the relation of tidal energy to the distribution of plankton species; and some hydrological themes. Four papers have appeared in Vol. xxvii, No. 2 of the *Journal* on the distribution and physical chemistry of iron in the sea, on the possibility of the existence of particulate ammonia in the sea and on some reflexions of phosphate distribution shown by fishery statistics. A review on the nutrient balance in the sea has been published elsewhere.

Mr F. A. J. Armstrong now undertakes the monthly hydrological cruises and the subsequent determinations of inorganic and total phosphorus. He is also adapting and improving other methods, such as that for nitrate, for use with Dr Harvey's photoelectric absorptiometer.

The echo-sounder has revealed a submarine declivity parallel with, and about two miles outside, Plymouth Breakwater. A study by Dr Cooper has shown that its height lies at a mean depth of 39 m. below L.W.S. and its height from foot to brow is about 10 m. It appears to represent a cliff cut during a period when the level of the sea stood at least 40 m. lower than to-day. The submerged banks of the estuarine channel of the combined Tamar and Plym are clearly evident for several hundred metres inshore of the coastal declivity.

Plankton

Mr F. S. Russell has continued the preparation for publication of his monograph on British Medusae. During the year Dr P. L. Kramp of the University Zoological Museum at Copenhagen spent a short time at Plymouth and kindly read through much of the manuscript and gave helpful advice.

Examination of the year's series of half-hour oblique hauls with the 2 m. stramin ring-trawl has not yet been completed by Mr P. G. Corbin. It is, however, evident that the numbers of young fish have again remained low, and *Sagitta* species have been generally scarce. Both *Muggiaea atlantica* and *M. kochi* occurred during the summer, and in the autumn small numbers of salps and doliolids were taken, as well as considerable numbers of the medusa, *Liriope*, an *elegans* water indicator. Other *elegans* water indicator species were, however, not numerous.

A paper on the post-larval *Ammodytes* species of the Celtic Sea and Plymouth area by Mr Corbin and Miss Vati will be published in Vol. xxviii, No 1 of the *Journal*. Four species of *Ammodytes* post-larvae occur. These belong to *A. lanceolatus*, *A. tobianus*, *A. marinus* and a fourth species of *Ammodytes*, the adult of which, it is concluded, is not yet known. With *A. cicerellus*, of which further adult specimens have been taken during the year, this makes a total of five *Ammodytes* species for the area.

A study has also been made by Mr Corbin of the distribution pattern of the scales on adult *Ammodytes* species. It has been found that the pattern in *A. tobianus* is quite distinct from that in *A. marinus*. This character, which

applies over the wide variation in the number of vertebrae occurring within the geographical range of *tobianus* and *marinus*, provides grounds for concluding that both are good species. There previously existed considerable divergence of opinion as to whether they were species, subspecies or races. The different patterns are recognizable in individual specimens. The two species may thus be identified without counting the number of vertebrae in a large sample, which was formerly necessary for their satisfactory separation.

Mr P. S. B. Digby, with a grant from the Development Fund, continued the work on the collections of smaller planktonic copepods made in the Plymouth area during 1947 and until June in 1948. On the basis of the relative numbers of the different stages of the various species and their size graphs, provisional conclusions can be drawn regarding the breeding and number of generations passed through in the course of the year. The observations have been made at the hydrographical station L 4, close to Plymouth, and the validity of the conclusions rests on proof that the changes observed at Plymouth occur in similar fashion over a large area, and are not unduly affected by movements of the water masses. Subject to these limitations we may say that for the species investigated—*Paracalanus*, *Pseudocalanus*, *Oithona*, *Temora* and *Acartia*—breeding is continuous in that nauplii are found throughout the year. The adults which live through the winter die out in February or March, having given rise to nauplii which produce a sparse population of adults of large size in March and April. The individuals of the following brood of adults are of smaller size and occur in May, June and July, and the next are of smaller size still and occur in August and September.

Thus it would appear that in the sea off Plymouth these copepods all pass through four generations in the year in a closely similar manner. It may well be that factors influencing survival of the nauplii and young stages of all the species together may serve to keep the breeding times of the population in step, when each species might have a different time if reared individually under laboratory conditions.

During the summer Mr Digby went to Spitsbergen, where he was based, mainly in Advent Bay, from 11 July to 10 September. A large number of plankton collections were made with vertical tow-nets and a modified Clarke-Bumpus Sampler to study the vertical distribution of plankton under conditions of continuous daylight.

Cultures of marine planktonic diatoms and flagellates have been maintained throughout the year and subcultures have been sent to other countries and other institutions in Britain for research purposes. A study, started at the Port Erin Marine Biological Station, of six of these marine flagellates has been completed by Dr Mary Parke and will be published in Vol. xxviii, No. 1 of the *Journal*. A form of reproduction in a palmelloid-phase, not previously described, is recorded for those species belonging to the Chrysophyceae. All six are new and four of them have been placed in three new genera.

Fauna and Flora of the Sea Floor

Mr D. P. Wilson has published in Vol. xxvii, No. 3 of the *Journal* a description of the development of the polychaete *Ophelia bicornis* Sav. and an account of his experiments in 1946 and 1947 on the settling reactions of the larvae of this species. These experiments were continued in 1948 with the object of obtaining further data from which the factor or factors responsible for initiating metamorphosis could more certainly be deduced. The earlier experiments had shown fairly conclusively that size and shape of the interstices among the sand grains, a purely physical environmental character, was the main factor responsible, but it was felt that further evidence was desirable in view of the important bearings these findings have on the ecology of larval settlement generally. The 1948 experiments, therefore, while on similar lines to the earlier ones, included tests with various non-marine sands, with artificial glass spheres (Chance's 'Ballotini') and with sand from the *Ophelia* grounds at Exmouth graded and recombined with an unnaturally large proportion of the smallest grains. The results obtained fully confirmed previous conclusions that physical size and shape of the sand grains is all important, while there was no indication whatever that anything in the nature of a soluble substance present in the natural sand plays a part in stimulating *Ophelia* larvae to metamorphose.

Difficulties in obtaining healthy fertilizations were experienced during the early part of the breeding season. After discussions with Dr Cooper it was decided to compare larvae reared in Channel water from the immediate vicinity of Plymouth with larvae from the same batches of eggs reared in western water from a region well to the west of the Isles of Scilly. In a few trial comparisons it was found that *Ophelia* larvae were healthier and lived longer in the western water than in the Channel water. This difference could not be due to food as both kinds of water had been passed through a Berkefeld filter and the larvae at the time were not feeding. However, the experiments were too few for definite conclusions to be drawn; it is proposed to continue them next year.

In the course of preparation of Part II of 'the distribution of *Gammarus* species in estuaries', Mr G. M. Spooner has examined some new collections from the Rivers Avon and Yealm to fill in gaps in the data previously obtained. A clearer picture is now available of the sporadic distribution of *G. chevreuxi* which, though plentiful in suitable points in all branches of the big watershed which includes the Plym, Tavy, Tamar and Lynher, appears to be completely missing from the Yealm and its branches, as well as from the Avon, and apparently from other South Devon rivers, for which records to date are all negative. Though it is a south-western species (with its range extending eastward to Hampshire and northward to north-east Ireland and Anglesey),

such an abrupt break in its distribution as occurs between the Plym and Yealm estuaries is difficult to explain.

Some further samples of *G. zaddachi oceanicus* from the west coast of Scotland, kindly sent by the late Mr R. Elmhirst, have been seen, indicating that this is a prevalent form in sea lochs at least as far south as Loch Duich opposite Skye. Examination of additional material of *G. locusta* from pure marine habitats suggests that a distinct form is separable in which the male antenna 2 has dense hair tufts in which many hairs are curled, and the female a shorter gnathopod 2 hand; but decision whether this is a habitat form or possibly a valid species awaits more information.

Some attention has been given to the distribution of *Corophium volutator* as an estuarine species, with the immediate result that a new species, hitherto confused with *volutator*, has come to light. The new species occurs at the top end of estuaries in low salinities, in a variety of situations, such as amongst clumps of *Cordylophora*, in the debris of reed beds, and in brackish ditches; but apparently not often in bare flat ground or open saltings pools as does *Corophium volutator*. So far it has been found in the Rivers Plym and Tamar. Immatures can be recognized from those of *C. volutator*.

Samples of *Corophium arenarium*, collected by Mr N. A. Holme on the Exe estuary, have been examined and additional characters distinguishing this species from *C. volutator* have been noted. The two species are confirmed as distinct, and all individuals can be separated, a point which the existing description leaves open to doubt.

Dr Mary Parke has published in Vol. xxvii, No. 3, her first paper on the British Laminariaceae, dealing with *Laminaria saccharina* (L). Lamour.

The occurrence in Plymouth Sound of a species of *Laminaria* new to Britain, *L. ochroleuca* De La Pylaie, has been recorded by Dr Parke. Its distribution in the Sound has been ascertained but so far it has not been found on any other part of the South Devon coast. A record has been kept of the colour change in the frond throughout the year and the times of rapid and slow growth have also been observed for comparison with the other species. Growth in this species is very similar to the growth in *L. digitata*. The gametophytes have been grown in culture from the zoospores and the young sporophyte stages obtained from them. The gametophytes and young sporophytes show little variation from those of the other British *Laminaria* species.

At the same time the opportunity was taken of testing whether certain algae secrete antibiotic substances which can inhibit the development of competitive algae and other cultures of *L. ochroleuca* were set up. To these were added pieces of living tissue of different brown algae. All cultures produced healthy gametophytes on which numerous sporophytes developed, as did those cultures without the addition of other algae; none of the gametophytes was decolorized by the addition of any one of the other species. These experiments

need to be repeated, however, using the zoospores of other *Laminaria* species and the fertilized oogonia of the Fucaceae.

Additions have been made to the collection of preserved specimens of marine algae being built up at the laboratory; the most interesting of these are *Desmarestia dudresnayi* Lamour. and *Carpomitra costata* Batt., since neither has been recorded since 1896. Further information has also been accumulated on the distribution and periodicity of reproduction of the marine algae of the Plymouth area.

Mr H. G. Vevers has now carried his investigation of the growth and reproduction of *Asterias rubens* over two breeding seasons and some of the results will be published in Vol. XXVIII, No. 1 of the *Journal*. In addition to the populations studied in 1947 a new population of starfishes was found in the spring of 1948 in Plymouth Sound. Although living in an area subject to a low winter temperature and to pollution by fresh water this population showed a very high percentage of large ripe gonads. As in the other populations it is considered that the high percentage of ovarian maturity in this population and the large absolute size of the ripe gonads is primarily correlated with the richness of the available food supply, which in this area consisted of a large bed of mussels. In general, the investigation has shown that the productivity of a starfish population is not related to age. Poorly-fed starfish survive and show little or no gonad maturing while well-fed starfish grow fast and reach breeding condition in their first year. The production of a large homogeneous population of starfishes depends upon the availability of a food animal which must not only be present in large numbers but whose mean size must be at an optimum to suit the size of the starfishes.

Preliminary work has been done on the development of an underwater camera for work at 70-100 m. This is designed to take a series of 40-45 photographs of the sea bottom at a single lowering, and it is hoped that by this means information may be obtained on the horizontal distribution of starfishes and other bottom-living animals.

An investigation has also been started on the breeding biology of *Amphioxus lanceolatus* in the Plymouth area.

Mr N. A. Holme, on a D.S.I.R. grant, has spent much of the year working on material collected from the Exe estuary in the summer of 1947. As a result of peculiar conditions arising from erosion of Dawlish Warren it has been possible to study the fauna of soils ranging from sand to mud, differences other than those directly due to the type of soil being eliminated. A paper giving the results of the survey is being published in Vol. XXVIII, No. 1 of the *Journal*.

In addition, preliminary attempts have been made at an evaluation of the quantity of animal life on the sea bottom. A new grab has been designed and built which takes rather better samples than those obtained with the Petersen Grab. During a cruise in Great West Bay in August 1948 the grab was worked on a variety of soils with success. The material collected is being

identified, and it is hoped that a note on the fauna of this area will be published shortly. The fauna of Great West Bay is rather poorer than that of the Plymouth area, but a number of interesting species have been recorded, including a specimen of *Lepidasthenia argus* Hodgson previously recorded only from Salcombe and from one locality near Plymouth.

Miss U. M. Grigg, also on a D.S.I.R. grant, has been working on the four species of Trochid molluscs common near Plymouth, *Monodonta lineata* (da Costa), *Gibbula cineraria* (L.), *G. umbicalis* (da Costa) and *Calliostoma zizyphinum* (L.): all are shore animals.

It appears that the change in shell shape from a flat cone to a tall tumid one occurs with size and is not conditioned by environment. The length of life is probably not more than two years. Males and females appear to be present in about equal numbers. The breeding season of the *Gibbula* species is in the early spring, *Calliostoma* breeds in May and June, and *Monodonta* in July and August. Attempts to rear the young, and to find where they metamorphose, have so far failed. The members of this family avoid a shifting substratum, turbid water, strong currents and low salinity. *Monodonta*, which has the most restricted habitat, is more common in the area than the accounts of its distribution would suggest.

Specimens of the deep-water *Gibbula magus* (L.), *Calliostoma papillosum* (da Costa) and the dwarf albino variety of *C. zizyphinum*, mentioned by S. Pace, have been obtained from localized collecting grounds where they do not appear to be common. No examples of *Gibbula tumida* (Montagu) or any of the three species of *Cantharus* recorded for the district have been observed.

Physiology of Marine Animals

Mr D. K. Hill has been continuing on a line of work which was started at Cambridge in the spring of 1948 concerning the nature of a change in optical opacity of non-myelinated nerve fibres resulting from stimulation. A first step in the attempt to discover the cause of this phenomenon has necessitated the construction of an apparatus with the aid of which the effect of electrical stimulation can be compared with any change in opacity that can be induced by chemical agencies, such as drugs known to affect the metabolism of nervous tissues (e.g. veratrine), or by changes in the ionic content of the fluid surrounding the isolated nerve. The evidence obtained in this way made it seem probable that the phenomenon could largely be accounted for by the swelling or shrinking of individual fibres in response to osmotic pressure or volume changes across the membrane. To test this hypothesis a direct measurement has been made of the alteration in diameter of a single giant fibre from *Sepia*. The change is very small, but it has proved possible to measure it: there is an increase in diameter of about 0.16 micron as the

result of 10,000 impulses passed down the fibre. It seems likely that the effect is largely due to the difference in volume between the hydrated sodium and potassium ions which are known to exchange across the membrane during activity. The next step will be to record the alteration in opacity of a nerve with a much higher speed than has been possible so far, and in this way to determine what happens during the interval while the action potential is passing.

Some preliminary experiments have been made by Mr G. M. Spooner to examine possible effects on organisms of radioactive elements present in solution in the water in which they are living. Certain isotopes emitting β -rays are being used. *Gammarus chevreuxi* kept in 25% strength sea water is a convenient invertebrate animal for investigating lethal and sterilizing doses. An approximate lethal dose for adults has been found. For the young the dose is rather less, especially if treatment starts two to three days before they are extruded from the mother's pouch. A much lower dose, however, is effective in causing sterilization of breeding adults.

Tests with a marine green flagellate (*Chlamydomonas* sp.) show a high resistance to treatment. Cultures persist with the activity of the medium of 100 μ curie per ml.

Further experiments testing the absorption of certain isotopes by different types of marine algae are in progress, using simple 'tracer' technique.

Fish and Fisheries

During the year, Mr E. Ford has continued his study of the anatomy and spatial form of the neurocranium in gadiform fishes. The growth centres of the supraoccipital, frontal plate, mesethmoid, prevomer, parasphenoid and basioccipital lie in the longitudinal vertical plane about which the neurocranium is bilaterally symmetrical. By sawing skulls in half along this plane, and then marking the position of these bone centres, the form of the polygon between them can be accurately determined in both linear and angular dimensions. This polygon is not only highly diagnostic of species, but is a very practical and informative means for drawing comparisons between species, according to a natural and strictly comparable set of coordinates. It is hoped that a first report on the work will soon be ready for publication.

Mr G. A. Steven has continued to work up the results of his investigations into the life-history and biology of the mackerel and a paper on 'Mackerel Migrations in the English Channel and Celtic Sea' was published in Vol. xxvii, No. 3 of the *Journal*.

Following upon these studies of the migrations a relevant study of the Newlyn deep-sea fishery has now been made. This reveals that, in general, the best catches are to be expected near the periphery of the areas of greatest

spawning intensity especially on the landward side. The reason why fishing is not successful actually in those areas of high spawning activity has not been established, but there is some evidence to suggest that mackerel in full spawning are at too great depths to be taken in the drift nets. Now that the Association's larger vessel is equipped with echo-sounding gear it is hoped that a survey of the spawning grounds at spawning time with the echosounder may yield useful data on this point.

It has also been found that by far and away the best catches are taken in what east-coast fishermen call 'yellow' water and Cornishmen call 'cowdung' water. This is water of a yellowish green colour that is not very common and in some years may not be found at all. When present it is rich in calanoid copepods. These, when preserved, often release into the preserving liquid certain pigments, possibly carotenoids, that cause the fluid to assume nearly the same hue as the 'yellow' water from which they were taken. But this, of course, also applies to calanoid copepods taken in waters of other colours. The problem of 'yellow' water is, therefore, being further investigated. At present the explanation seems to be that the presence of extra large numbers of calanoid copepods attracts mackerel to the spot, and that the colours of the fish and those of copepod pigments (either in the living animals or in faecal products) combine to produce the characteristic 'yellow' colour.

It has been established that the shoreward migration of the mackerel in this area is not a spawning migration; but neither is it a feeding migration, as has also been suggested. There is nothing to support the belief that the fish come inshore *in order to feed* because they pass through and leave behind them an abundance of food on the way. There is merely a change of diet from predominantly planktonic crustacea in offshore waters to a diet consisting largely of small fish in inshore localities. A detailed study of the distribution of mackerel food on the fishing grounds, and of the feeding habits of the fish, is nearing completion and is now being written up.

The Library

The thanks of the Association are again due to numerous foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those who have sent reprints of their papers, which are much appreciated.

The Association is also very grateful to Sir Sidney Harmer, F.R.S., for his gift of a collection of scientific papers, including a long run of Monographs of the Siboga Expedition, and to the late Prof. W. Garstang, especially for a copy of Jonathan Couch's *Cornish Fauna*, annotated and illustrated by Couch himself.

Published Memoirs

Vol. XXVII, No. 2, of the *Journal*, was published in April 1948, Vol. XXVII, No. 3, appeared in December, and Vol. XXVIII, No. 1, is nearing completion.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

- ATKINS, W. R. G., 1947. A suggested repellent for Schistosome Cercariae. *Journ. Hygiene*, Vol. 45, 1 p.
- ATKINS, W. R. G., 1948. Note on the spectroscopic and biological detection of potassium in sea water and 'potassium-free' artificial sea water. *Journ. du Conseil*, Vol. xv, pp. 169-72.
- BURTON, MAURICE, 1948. The ecology and natural history of *Tethya aurantium* Pallas. *Ann. & Mag. Nat. Hist.* (12), Vol. 1, pp. 122-30.
- BURTON, MAURICE, 1948. The synonymies of *Haliclona angulata* (Bowerbank) and *H. arcoferus* Vosmaer. *Ann. & Mag. Nat. Hist.* (12), Vol. 1, pp. 273-84.
- COOPER, L. H. N., 1948. A submerged ancient cliff near Plymouth. *Nature*, Vol. 161, p. 280.
- COOPER, L. H. N., 1948. The nutrient balance in the sea. *Research*, Vol. 1, 6 pp.
- COOPER, L. H. N., 1948. Significant figures in analytical chemistry. *The Analyst*, Vol. 73, No. 870, pp. 508-9.
- COOPER, L. H. N. & STEVEN, G. A., 1948. An experiment in marine fish cultivation. *Nature*, Vol. 161, p. 631.
- DAS, S. M., 1948. British Folliculinidae (Ciliata, Heterotricha). *Nature*, Vol. 162, p. 534.
- GROSS, F., COOPER, L. H. N. & STEVEN, G. A., 1948. Marine fish cultivation. *Nature*, Vol. 162, p. 378.
- HODGKIN, A. L. & KATZ, B., 1949. The effect of sodium ions on the electrical activity of the giant axon of the squid. *Journ. Physiol.*, Vol. 108, pp. 37-77.
- KATZ, B., 1949. Neuro-muscular transmission in invertebrates. *Biol. Reviews*, Vol. 24, pp. 1-20.
- KELLEY, D. F., 1949. The mystery of the bass: a report on three years' study of its habits. *Angling*, Vol. xi, pp. 79-83.
- LEBOUR, MARIE V., 1949. Two new Pycnogonids from Bermuda. *Proc. Zool. Soc.*, Vol. 118, pp. 929-32.
- LEBOUR, MARIE V., 1949. Some new Decapod Crustacea from Bermuda. *Proc. Zool. Soc.*, Vol. 118, pp. 1107-17.
- LOWENSTEIN, OTTO & ROBERTS, T. D. M., 1948. Oscillographic analysis of the gravity and vibration responses from the labyrinth of the Thornback Ray (*Raja clavata*). *Nature*, Vol. 162, pp. 852-3.
- LOWENSTEIN, OTTO, 1948. Oscillographic analysis of the non-acoustic functions of the vertebrate ear. *Nature*, Vol. 161, pp. 652-4.
- NICOL, J. A. C., 1948. The giant nerve-fibres in the central nervous system of *Myxicola* (Polychaeta Sabellidae). *Quart. Journ. Micro. Sci.*, Vol. 89, pp. 1-45.
- PARKE, MARY, 1948. *Laminaria ochroleuca* De La Pylaie growing on the coast of Britain. *Nature*, Vol. 162, pp. 295-6.
- RUSSELL, F. S., 1948. Pure and applied science of the sea. (Being the Ludwig Mond Lecture, delivered at the University of Manchester on March 11, 1948.) *Science Progress*, Vol. xxxvi, pp. 423-35.

- RUSSELL, F. S., 1948. Alexander Sand, 1901-45. *Obituary Notices of Fellows of the Royal Society*, Vol. v, pp. 803-14.
- SPROSTON, NORA G., 1948. On the genus *Dinobothrium* van Beneden (Cestoda), with a description of two new species from sharks, and a note on *Monorygma* sp. from the electric ray. *Parasitology*, Vol. xxxix, pp. 73-90.
- SPOONER, G. M., 1948. The British species of Psenine wasps. (Hymenoptera: Sphecidae). *Trans. Roy. Entomol. Soc.*, Vol. 99, pp. 129-72.
- STEVEN, G. A., 1949. The mackerel: new light on its migrations and habits. *Discovery*, March 1949, 3 pp.
- TATTERSALL, OLIVE S., 1949. A rare species of Mysid from the Plymouth area. *Nature*, Vol. 163, p. 450.

Membership of the Association

The total number of members on 31 March 1949 was 505, being 47 more than on 31 March 1948; of these the number of life members was 72 and of annual members 433. The number of Associate members is now six, Dr W. T. Calman, C.B., F.R.S., Mrs S. W. Kemp, Mr J. L. Parkinson and Mr R. A. Todd having been elected during the year and Mr G. H. Wailes having died.

It is gratifying to record that since March 1945 the total membership of the Association has been increased by 139.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Capital Grants. The Council wish to record their thanks to the Development Commissioners for generous capital grants from the Development Fund towards the cost of rebuilding the East Wing, the completion of the research vessel *Sula*, and the modification of the *Sabella*.

Private Income. The Council gratefully acknowledge the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), The Ray Lankester Fund (£20), the Cornwall Sea Fisheries Committee (£10), the Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10s.), Leeds (£20), Durham (£10. 10s.), Manchester (£10. 10s.), Nottingham (£10. 10s.), Exeter (£10. 10s.), Leicester (£10. 10s.), Southampton (£10. 10s.), Sheffield (£5), and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1949-50:

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G. P. BIDDER, Sc.D.	Admiral Sir AUBREY C. H. SMITH, K.B.E.,
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C. F. HICKLING, Sc.D.
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To retire in 1952

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£47,695 7 10

REPORT OF THE AUDITORS TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Prudential Buildings, George Street, Plymouth.

2nd May 1949.

PRICE, WATERHOUSE & CO.

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1949

	£	s.	d.	£	s.	d.	£	s.	d.
To SALARIES, including Association's contributions to Superannuation Scheme and National Insurance ...	15685	12	9						
" LABORATORY AND BOATS' CREWS' WAGES, including National Insurance, contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance ...	12406	5	4						
" UPKEEP OF LIBRARY ...	273	8	11						
" SCIENTIFIC PUBLICATIONS, LESS SALES ...	1199	7	3						
" UPKEEP OF LABORATORIES AND AQUARIUM: Buildings and Machinery ...	547	5	0						
Electricity, Oil, Gas, Coal and Water ...	441	4	6						
Chemicals and Apparatus ...	821	9	3						
Fire Insurance, Tithe, Ground Rent and Rent of Store ...	130	0	11						
Travelling Expenses ...	528	6	1						
Audit Fee ...	10	10	0						
Stationery, Postages, Telephone, Carriage and Sundries ...	737	9	7						
Specimens ...	214	10	9	3430	16	1			
" MAINTENANCE AND HIRE OF BOATS: Petrol, Oil, Paraffin, etc. ...	364	8	4						
Maintenance and Repairs to Nets, Gear and Apparatus ...	1752	12	5						
Purchase of Materials for Nets, etc. for Re-sale ...	769	19	4						
Boat Hire, Collecting Expenses and Upkeep of Truck ...	177	6	9						
Insurances ...	645	6	11						
" ENTERTAINMENT EXPENSES ...	3769	13	9						
" BANK CHARGES ...	39	11	3						
" TRANSFER TO MACKEREL RESEARCH FUND ...	16	18	8						
" TRANSFER TO VESSELS HIRE AND CAPITAL EXPENDITURE FUND ...	—	—	—						
" BALANCE, BEING EXCESS OF INCOME OVER EXPENDITURE FOR THE YEAR ...	240	6	8						
(Cr)									
Note: No provision is made for replacement of Fixed Assets.									
By GRANTS AND TABLE RENTS: Ministry of Agriculture and Fisheries Grant from Development Fund ...	30000	0	0						
Fishmongers' Company ...	500	0	0						
Miscellaneous (including British Association £50, Royal Society £50, Physiological Society £30, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10s. od., Leeds £20, Durham £10. 10s. od., Exeter £10. 10s. od., Leicester £10. 10s. od., Manchester £10. 10s. od., Nottingham £10. 10s. od., Southampton £10. 10s. od. and Sheffield £5; Imperial College £10, Ministry of Works £104, and Ray Lancaster Fund £20) ...	1206	14	7	31706	14	7			
" SUBSCRIPTIONS (excluding Subscriptions received in advance) ...	430	1	1						
" FEES FOR TESTS OF MATERIALS ...	30	0	0						
" SALES: Specimens ...	2216	8	11						
Photographs ...	—	—	—						
Fish ...	366	12	2						
Nets, Gear and Hydrographical Apparatus ...	933	15	3						
" INTEREST ON INVESTMENTS ...	3516	16	4						
" SALE OF DR. M. V. LEBOUR'S BOOK ...	26	5	10						
" SALE OF 'PLYMOUTH MARINE FAUNA' ...	6	17	6						
" AQUARIUM: Admission Fees ...	1463	14	3						
Sale of Guides and Postcards ...	108	16	2						
Less: Maintenance of Buildings ...	1572	10	5						
Printing Guides and Tickets ...	53	16	0						
Food ...	79	9	4						
Wages ...	90	12	0						
	83	14	0						
" TRANSFER FROM BIOLOGICAL INVESTIGATIONS ON ALGAE FUND ...	307	11	4	1264	19	1			
				8	1	3			
				£37,002	0	8			

CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL *SCOMBER SCOMBRUS* L.

II. A STUDY OF THE FISHERY IN THE SOUTH- WEST OF ENGLAND, WITH SPECIAL REFERENCE TO SPAWNING, FEEDING, AND 'FISHERMEN'S SIGNS'

By G. A. Steven, B.Sc., F.R.S.E.

Zoologist at the Plymouth Laboratory

(Plate I and Text-figs. 1-6)

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INTRODUCTORY SURVEY

In a previous paper (Steven, 1948), brief accounts are given of three distinct mackerel fisheries that at one time existed in the south-west of England—an inshore fishery in the English Channel carried on from Plymouth, a deep-sea fishery from Newlyn, Cornwall, and an inshore fishery from Newlyn and some other Cornish ports. One of these fisheries, the Plymouth one, no longer exists. After a few years of considerable activity following the termination of the 1914-18 war, this fishery collapsed in 1924 (Table I) and came entirely to an end a few years later. The small quantities of mackerel landed at Plymouth in subsequent years have been incidental catches by vessels fishing for herrings or pilchards.

The Cornish inshore fishery took place mainly at no great distance to sea—on the northern shore of the Devon-Cornwall peninsula and was carried on chiefly by small local craft, both wind- and motor-driven; but a number of visiting east-coast drifters used also to participate, especially during January and February, when stormy weather prevented their going very far to sea in search of other shoals in deeper waters beyond the Scilly Islands (Steven, 1948,



p. 520, fig. 3). Soon this fishery too fell upon hard times and the small local craft gradually abandoned mackerel fishing. In 1931 the local Fisheries Officer reported to the Cornwall Sea Fisheries Committee that, so far as local vessels were concerned, the fishery had arrived almost at the point of extinction.

The failure of both the Plymouth and Newlyn inshore fisheries was due to a decline in the quantity of fish in nearby waters, combined with low prices which made small catches unremunerative. The fall in fishing yield in those years is clearly reflected in the mean weight of fish per landing by the local vessels engaged in the Newlyn fishery. At no time¹ from 1906 (when reliable returns first became available) until 1927 did this average fall below 10 cwt. (Text-fig. 1), and was generally much higher. But with the single exception of 1928 the 10 cwt. figure was never again reached; in fact the individual

TABLE I. QUANTITY OF MACKEREL LANDED AT PLYMOUTH,
1919-38 INCLUSIVE (IN CWT.)

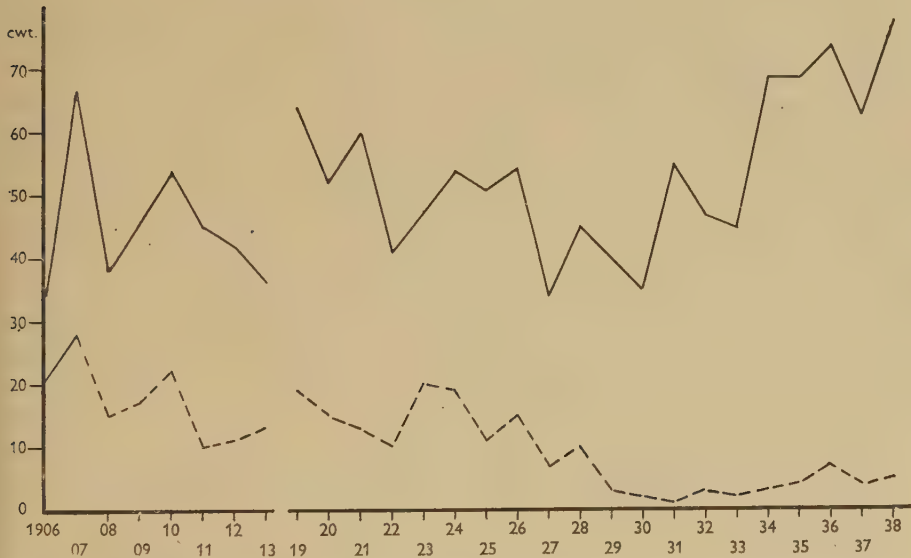
Year	Quantity	Year	Quantity	Year	Quantity
1919	15,521	1926	4080	1933	2200
1920	33,618	1927	3080	1934	1859
1921	18,117	1928	2582	1935	2401
1922	18,198	1929	3005	1936	2670
1923	15,551	1930	3109	1937	1669
1924	5,366	1931	3101	1938	1156
1925	5,229	1932	4709		

landings were generally less than half that amount. These weights are a reasonably accurate index of the quantity of fish available on the fishing grounds because landings by local vessels represent only one night's fishing.

Many of the steam drifters reacted to the decline in the inshore fish stocks by postponing their arrival in Newlyn until about the beginning of March in each year, when weather conditions permitted them to proceed at once to more distant fishing localities in the open sea well beyond the Scilly Islands, where better catches were to be had on different bodies of fish migrating in from the westward. But even as late as 1930 some steamers still endeavoured to obtain satisfactory catches in nearby localities in January and early February, but without success, and they worked at a loss until better weather in March enabled them to proceed to the distant grounds where better results were obtained. This was the very last year in which steam drifters fished from Newlyn as early as January. Since that time the steam-drifter fishery has opened invariably on the deep-sea grounds not earlier than the last days of February or the first days of March. But even the deep-sea grounds failed to provide satisfactory returns for all the participating craft and many of them gave up mackerel fishing altogether (Table II), their numbers falling from 90 in 1920 to 23 in 1940, the last year of normal fishing.

¹ War years excepted.

The steam drifters that did not give up fishing strove to maintain their catches at remunerative levels by working at ever increasing distances from land until eventually, from about 1927 onwards, it became the regular custom of most of the fleet to open the fishery every spring on grounds as much as 100 miles or more to seaward of the Bishop Rock (Scilly Islands) on bearings lying generally between W.N.W. and W.S.W.



Text-fig. I. Mean weight in cwt. of mackerel per landing at Newlyn in the years 1906-38 inclusive: (—), by steam drifters; (---), by local craft.

TABLE II. NUMBER OF STEAM DRIFTERS FISHING FROM NEWLYN IN THE YEARS 1920-40 INCLUSIVE

Year	No.	Year	No.	Year	No.	Year	No.
1920	90	1926	82	1931	47	1936	31
1921	60	1927	74	1932	43	1937	23
1922	80	1928	60	1933	43	1938	27
1923	80	1929	55	1934	35	1939	25
1924	68	1930	52	1935	34	1940	23
1925	87						

Daily landings from these distant grounds obviously became impossible, so the practice of preserving the fish in ice was extended and improved to enable the ships to stay at sea for more than one night at a time on each fishing trip. Single landings at the beginning of the season, therefore, came to represent as many as 4 nights' fishing.

At the same time the fishing capacity of each drifter was also undergoing an important change. Before the war of 1914-18 the nets used by those craft

were of a type known as 'fly nets' and had a standard size of about 20 yd. length and 5 yd. depth. On resumption of fishing after peace returned a larger 'footrope net' began to be introduced which is about 33 yd. long and just over 6 yd. deep. By about 1933 the old type had been almost entirely replaced by the new. The number of nets in each fleet remained unchanged at approximately 180. The fishing area of each drifter's fleet of nets was therefore almost exactly doubled, rising from approximately 18,000 sq. yd. to approximately 36,000 sq. yd.

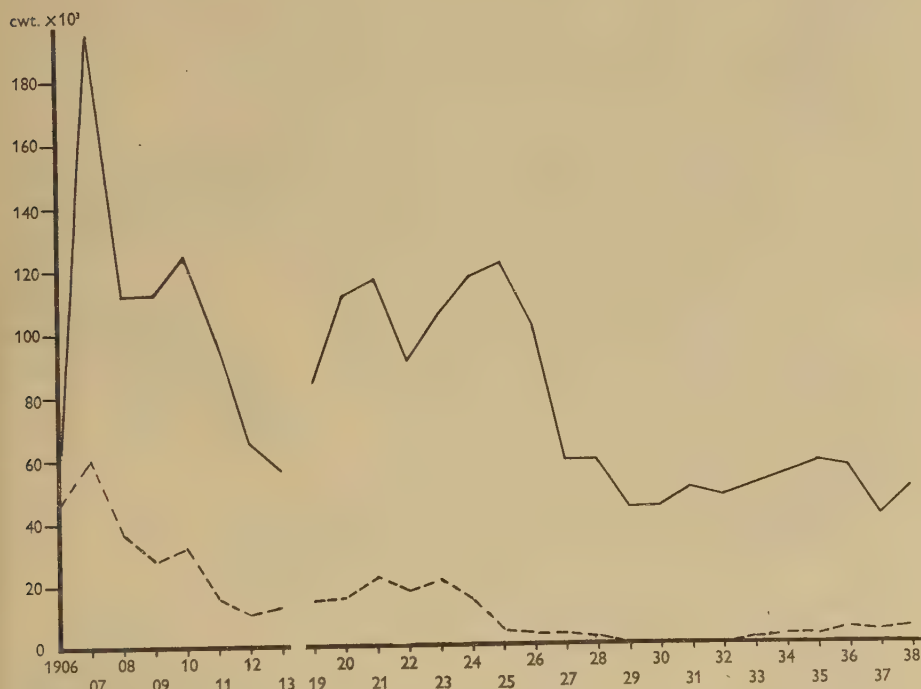
By these means a reduced fleet of little more than a score of drifters was able to make ends meet and continued to operate a small deep-sea mackerel fishery from Newlyn during the months of March-June until the outbreak of the second World War put an end to their activities.

Unlike the daily landings of the small local vessels, therefore, the mean weight of fish in landings by the steam drifters from about 1927 onwards, is not a true reflexion of the quantity of fish available on the grounds. Daily landings are possible only over short distances. But scarcity of fish on nearby grounds caused the participating steam vessels to go farther and farther away from port in search of remunerative catches, and the additional costs of extra steaming were offset by increasing the fishing capacity of the nets and by spending more time on the fishing grounds. In such circumstances the mean weight of fish per landing will tend not to decrease but to increase as fish become scarcer. This is what actually happened in the Newlyn Deep-Sea Mackerel Fishery in the 12-year period from 1927 until 1938. From inspection of Text-fig. 1 (and Appendix I) it will be seen that during those years there was a fairly steady increase in the average weight of fish per steam-drifter landing from 34 cwt. in 1927 to 78 cwt. in 1938.

There was no corresponding increase in the total yield of the fishery. This, in fact, from 1927 onwards, remained remarkably constant (Text-fig. 2), because, although the mean weight per landing increased, the number of landings decreased. This decrease in the number of landings was due only in part to the increased length and duration of the fishing trips. Another and more important cause was a gradual decline in the public demand for mackerel. This is indicated by their market value on first sale (Table III), which fell steadily from 19s. 5d. per cwt. in 1929 to only 9s. 11d. in 1936. There was a slight recovery to 13s. 8d. in 1937, but another fall to 12s. 4d. in 1938.

More mackerel could have been landed by the existing fleet if the demand for them had existed; for from about 1930 onwards the skippers of steam drifters working from Newlyn voluntarily agreed from time to time to stay in port for from 1 to 3 days after each landing in order not to cause a glut of unwanted fish on a sluggish market. In some years approximately 20% of possible fishing time was lost in this way. The Statistical Tables of Sea Fisheries in England and Wales contain data covering the total landings of mackerel at Newlyn and the total number of landings by the different kinds of vessels, but no information is given either with the Tables or in the Official Reports (1906-38)

concerning such changes in the fishery as have been briefly described above. Unfortunately, therefore, the official statistics concerning the Newlyn deep-sea fishery for mackerel have little or no biological significance. Important



Text-fig. 2. Total landings of mackerel at Newlyn (in thousands of cwt.) in the years 1906-38 inclusive: (—), by steam drifters; (---), by local craft.

TABLE III. AVERAGE VALUE OF MACKEREL PER CWT. IN ENGLAND AND WALES FOR THE YEARS 1919-38 INCLUSIVE¹

Year	Value	Year	Value	Year	Value	Year	Value
1919	39s. 10d.	1924	17s. 9d.	1929	19s. 5d.	1934	11s. 3d.
1920	15s. 1d.	1925	16s. 4d.	1930	17s. 9d.	1935	11s. 7d.
1921	21s. 6d.	1926	17s. 1d.	1931	14s. 7d.	1936	9s. 11d.
1922	16s. 9d.	1927	19s. 5d.	1932	13s. 9d.	1937	13s. 8d.
1923	15s. 10d.	1928	17s. 2d.	1933	12s. 3d.	1938	12s. 4d.

¹ From Statistical Tables of Sea Fisheries.

factors other than the availability of fish on the fishing grounds have greatly influenced both the number and size of individual landings and the total yields—factors that have not been taken into consideration during the compilation of the tables nor recorded with them.

POSITION OF THE FISHING GROUNDS IN RELATION TO SPAWNING AREAS

The Newlyn deep-sea fishery takes place on fish that are moving landwards from the west. While still far off-shore most of them spawn. Heaviest spawning occurs in April in an extensive area of sea overlying the outer (seaward) part of the continental plateau near the 100-fathom contour (Corbin, 1947). Within this area there are two centres of maximal spawning intensity, one lying 40–100 miles south of Ireland and the other 50–80 miles south-west of Bishop Rock.



Text-fig. 3. Distribution of mackerel eggs (1–1000; 1001–5000; 5001–10,000; > 10,000) and young stages in the Celtic Sea in April, 1938. Reproduced from Corbin, 1938, p. 74. For further explanation see text.

The general shape and extent of those spawning areas in April 1938—a typical year—are clearly shown in Corbin's fig. 5A (1947, p. 74) reproduced here as Text-fig. 3 (except for the omission of a coloured patch over the westernmost stations where young stages were recorded). The numerals in general refer to numbers of eggs, taken in half-hour oblique hauls with the 2 metre stramin trawl by the method described by Russell (1930, 1935). Some, however, attached to the westernmost stations, refer to the planktonic young stages—such as the lower of a pair, or single numbers outside the egg limit (*vide* the original for more exact details).



Text-fig. 4. Mackerel spawning grounds and the locus of mackerel fishing by Newlyn-based steam drifters: (A), in April, 1938; (B), in May-June, 1938. Stippling indicates density of mackerel eggs, as in Text-fig. 3.

Corbin's charts of the spawning ground for 1938 are copied in Text-fig. 4 with the number of eggs and young stages omitted, but having inserted upon them the positions in which ten drifters were fishing during the time that the survey was being carried out. Every 'shot' by each of those drifters is indicated by one dot in the position in which it was made. Fishing by those ten selected vessels was fully representative of the activities of the full fleet of twenty-seven vessels. Reference to the chart (Text-fig. 4A) clearly shows that the fishing fleet was at the time concentrating its attention upon a well-defined area between, and slightly to landward of, the two chief spawning centres. This means, of course, that the best catches were to be had there. It is remarkable, to say the least, that mackerel fishermen should so unerringly have found this particular fishing ground though quite unaware of the presence of any intensive spawning nearby, especially as these grounds lie right out in the open sea 130 miles or more from port.

Corbin (1947, p. 72) has shown that as the season advances the locus of spawning moves eastwards and decreases in intensity. At the same time the locus of greatest fishing activity also moves eastward (Steven, 1948, p. 523, fig. 4). It has not been possible in any year to make frequent surveys of the spawning areas at brief and regular intervals, but a second survey was made during the period 31 May–5 June 1938. The centres of maximal spawning were then in the positions shown by the dark stippling in Text-fig. 4B. On this chart the activities of the fishing fleet are also shown by dots indicating the positions in which actual 'shots' were made by representative ships during the first fortnight of June 1938. Here again, best fishing was found near the landward periphery of the chief spawning centres. The reason why fishing is not concentrated between them, as in April, is the presence of the Scilly Islands and the 'toe' of Cornwall in the very place where, in their absence, best fishing would be expected; for since good catches are obtained on the periphery of a spawning centre, the very best results of all should be found in a locality which forms part of the peripheries of two separate spawning grounds overlapping at their edges. The position of the highest fishing intensity in April fulfilled this condition.

It is quite clear from the fishing fleet's activities that best fishing is to be found near, but not on, the centres of maximal spawning intensity. No explanation for this can be given. The most probable reason is either that the fish do not swim actively enough to be caught in the drift nets or that they remain too deep to be reached by them. Ehrenbaum (1923, p. 5) records that Holt, in a private communication to him, expressed the conviction that mackerel in full spawning do not rise to the surface. Collins (1883, p. 277) also states that mackerel in North American waters sink during the season of reproduction and rarely appear in shoals at the surface. It should now be possible to obtain definite information on this point by investigating the spawning centres and fishing grounds with a suitable echo-sounder. Un-

fortunately, none was available on any of the ships with which these researches in the Celtic Sea were carried out. Arrangements are now being made for echo-sounder surveys to be carried out as soon as circumstances permit. Until this is done one can do no more than note the possibility that while spawning in deep water the fish may be either deep or relatively quiescent, or even both.

Since the fishing fleet does not catch spawning fish in the first part of the season, very few ripe mackerel arrive on the fish markets during the months of March and April. It is not until May and later that appreciable numbers of fish containing small quantities of ripe ova and sperm are landed. The explanation for this appears to be that those fish that have not yet completely spawned are now in much shallower water and cannot go down very deeply to do so. The result is that some spawning fish can now be taken in drift nets on fairly active spawning centres even though best fishing is still to be had on the periphery of such centres.

When the two inshore fisheries existed they depended on unripe fish that were in the first stages of migration to the spawning ground, i.e. they, too, worked on non-spawning populations.

Having spawned off-shore, the mackerel perform a return migration to the coast (Steven, 1948, p. 524). This return migration is not, therefore, a spawning migration as has been supposed for so long. It is simply a post-spawning anadromous migration during which the fish are actively feeding; nevertheless it cannot be said that they come inshore *in order* to feed.

THE SPAWNING OF THE MACKEREL

Spawning takes place throughout the Celtic Sea during the period March till July. It increases very rapidly in intensity after the start, and by mid-April reaches a peak which lasts until May. Thereafter it decreases, until by the end of July it is only very slight. In the English Channel and also in the Irish Sea this slight residual spawning continues until August and even, in some years, until September (Corbin, 1947, p. 71).

This long-drawn-out spawning season is due, in part at least, to the fact that various populations of mackerel, converging on their off-shore spawning grounds from different winter quarters, both near and far away, do not all arrive there at the same time. When spawning activity is at its greatest—in the western part of the Celtic Sea in April—fish that wintered in the English Channel are still on their way westward (Steven, 1948, p. 520, fig. 3), and not yet fully ripe. It seems possible that this spread-over may be related not only to the different lengths of the migratory journeys but also to differences in the environmental conditions, particularly of temperature, in which the fish spend the winter. According to Cooper's analysis of such temperature data as exist for these areas (Appendix II, pp. 577–81), the waters over the greater part of the Celtic Sea are isothermal down to about 120 m. and in most years

have appreciably higher temperatures than those of the Hurd Deep where many if not most of the Channel mackerel spend the winter. Most of the Atlantic Slope mackerel, however, spend the winter below the 120 m. level but they, too, unless they go very deep indeed—which is unlikely—are subject to warmer conditions than the English Channel population. Observations in 1927 and 1932 reveal that the mean winter temperature along the 150 and 200 m. contours in those years was about 0.9°C . higher than the mean temperature at the Hurd Deep; only at 500 m. in 1932 and at 800 m. in 1927 (position $50^{\circ} 34' \text{N.}; 11^{\circ} 17' \text{W.}$) were Hurd Deep temperatures reached. Deep-water observations are also available for 1929, but Cooper regards that year as an exceptional one. Atlantic Slope water in that year was, at 200 m. depth, $2.5\text{--}2.8^{\circ}\text{C}$. warmer than the Hurd Deep; even at 986 m. the Atlantic Slope water was still 0.7°C . warmer. It seems clear, therefore, that mackerel wintering on the floor of the Celtic Sea, and in considerably deeper water at the outer edge of the continental plateau, are normally subjected to appreciably warmer conditions than others that spend the winter in the English Channel. Still others wintering near the bottom in the Smalls and Saltees areas will be also subjected to temperatures at least as low as those of the Hurd Deep.

Mackerel wintering around the various banks, knolls and gullies on the floor of the Celtic Sea, and in considerably deeper water at the edge of the continental plateau, are therefore not only nearer the spawning ground but are subjected to appreciably warmer conditions during their demersal period than others that spend the winter in the English Channel and in the Smalls and Saltees areas. It seems reasonable to suppose, therefore, that it is those fish that spend their demersal period in localities near the spawning ground, where also the warmer conditions prevail, that give rise to the early intensive spawning activity, followed by others from the more distant and also colder winter localities. There is also a possibility (supported by Cooper's theory of cascading waters from the shelf area down the side of the continental slope) that there may be a concentration of planktonic food organisms—chiefly copepods—at considerable depths along certain parts of the slope in February and March, especially in colder winters. Mackerel wintering in such localities, therefore, may also be better nourished (Cooper & Vaux, 1949).

Differences in winter temperatures may also be the factors underlying the later date of maximum spawning intensity on the chief North Sea spawning ground in the Skagerrak. Here (Ehrenbaum, 1914, p. 18; 1923, p. 11) the chief maximal spawning activity takes place a month later than in the Celtic Sea. It may be significant, therefore, that North Sea mackerel spend the winter in the vicinity of the Great Fisher Bank and northwards along the Norwegian Channel at least as far as the Viking Bank where winter temperatures are in general as much as $2\text{--}3^{\circ}\text{C}$. lower than those found in the Celtic Sea (Appendix II).

Another important factor contributing to the great spreadover of spawning

activity in both space and time is that in every individual female the eggs mature in successive batches that are spawned one after the other during an extended period, the exact duration of which is not known. Ripe translucent eggs appear in the ovary distributed widely and irregularly amongst still unripe yellowish ova in earlier stages of development. This gives rise to a peculiar speckled appearance that, for want of a better term, has been called the 'plum-pudding' stage (Le Danois, 1938, p. 22), of which an illustration is given in Pl. I, fig. 1. These ripe ova are dehiscent into the lumen of the ovary which then, on superficial examination, shows no trace of ripe eggs. Their presence can be ascertained only by opening up the ovary and examining the lumen in which a few ripe eggs will nearly always be found even after any particular batch has been shed. These must, however, be carefully looked for; a quick and superficial glance may easily miss them. An ovary that contained numerous ripe eggs in its lumen, but showed no external evidence of their presence, is illustrated in Pl. I, fig. 2. The existence of ovaries in this condition indicates that the final stages of the ripening process take place discontinuously in successive batches of eggs. Were the process a uniform and continuous one ripe eggs would always be visible externally in smaller or larger numbers throughout the whole period from the time that the first eggs ripen until the ovary is fully spent.

This mode of ripening of the eggs in mackerel ovaries is in marked contrast with the condition found in the herring, where all the eggs that are to be spawned in any one spawning season ripen more or less simultaneously, giving rise to the well-known 'mazy' condition in which large numbers of fully ripe eggs can be obtained from a single female at one time. This condition is never found in mackerel. Only a relatively small number of fully ripe eggs is ever present in a mature female at any time and a condition of easily recognized 'maziness' does not occur.

It was probably a more intimate and accurate knowledge of the ripening process in the ovary of the herring than of the mackerel that led Cunningham to make the misleading generalization (1889, p. 25): that in species of fish that swim in shoals and have pelagic and migratory habits the process of spawning is approximately simultaneous throughout the whole population in a given locality, proceeds very rapidly when once begun, and is limited definitely to one short period of the year. This generalization he wrongly applies to the mackerel in which he says: 'all the reproductive products in a given fish are matured and shed within a short space of time.'

The slightly later observations of Moore (1899, p. 5), however, are completely at variance with Cunningham's findings and in full agreement with the results of the present investigations. Moore draws attention to the fact that, in the same run of fish, individuals in very different conditions of maturity are found. The reason for this he very clearly points out to be due to the fact that 'the mackerel matures only a portion of the generation of eggs at one time',

as a result of which the ovary 'becomes spotted all over, both externally and on the internal lamellae with translucent spots due to aggregations of the clear eggs'. This very early description of the 'plum-pudding' stage, and how it arises, appears not to have received from subsequent workers the attention it deserves.

Correlated with the extended spawning period in the female there is, in the male, a correspondingly long period during which ripe sperms are present in the testes. The male differs from the female in that from the time that ripe sperms first appear at the beginning of the season an appreciable amount of ripe sperm is always present until the fully spent condition is reached. As in the female, however, the quantity of ripe sexual products present in a male fish at any particular time is always relatively small. Ripe males are generally present in small numbers in commercial catches before ripe females appear in them (Table IV).

TABLE IV. PERCENTAGE OF FISH (IN COMMERCIAL CATCHES BY STEAM DRIFTERS) IN DIFFERENT MONTHS CONTAINING RIPE SPERM OR EGGS

Figures in brackets are the total numbers examined during three fishing seasons (1937-39).

	Males	Females
March	5.9 (584)	0.0 (570)
April	20.6 (569)	7.9 (625)
May	62.5 (578)	52.2 (554)
June	52.8 (625)	47.6 (464)
July	14.4 (223)	17.3 (185)

It will be seen from the table that the two sexes appear in the catches in approximately equal numbers.

FOOD AND FEEDING

Adult mackerel spend part of each year in winter quarters on or near the sea-floor in the vicinity of banks and gulleys distributed over wide areas from shallow to deep water. In the English Channel, demersal concentrations of mackerel are found hard by the Vergoyer Bank off Boulogne, and by the numerous small sandbanks near Dieppe in only a few fathoms; and along the sides of the Hurd Deep in rather more than 40 fathoms. Elsewhere in the south-western area they occur at various depths in the neighbourhood of the Smalls and Saltees, around various banks and shoals on the floor of the Celtic Sea, and even along the Continental Slope itself, where they are regularly caught by British and other trawlers in depths of well over 100 fathoms 'west of Great Sole Bank' and elsewhere, especially in late February and March.

Amongst the mackerel that winter on the bottom in the English Channel fish with packed stomachs are seldom found. On the other hand, not all of them are empty. The fish, therefore, though not feeding voraciously, are not entirely fasting.

In the Plymouth region 753 mackerel were caught by trawl on or near the

sea-floor in the months of January–April during the years 1936–39. Of these 67% contained food consisting chiefly of *Nyctiphanes couchi*, mysids, small teleosts, and crangonids, but various other organisms were also represented (Table V).

It is obvious that while on or near the bottom in the English Channel the mackerel were feeding on such organisms as were suitable and available to them. By contrast, the stomachs of mackerel caught in drift nets near the surface in January have been almost entirely devoid of food. A few (just under 5% of the 138 fish examined) have contained traces of phytoplankton embedded in mucus and very occasionally traces of planktonic crustacea (copepods) have been present. Rather more plant material appears in the stomachs in February

TABLE V. PERCENTAGE OF BOTTOM-CAUGHT FISH (PLYMOUTH AREA) CONTAINING IN THEIR STOMACHS ONE OR MORE OF THE ORGANISMS LISTED BELOW

Name of organism	Percentage of stomachs in which found (to nearest whole number)
<i>Nyctiphanes couchi</i>	31
Mysids	26
Small teleosts	15
Crangonids	11
Polychaetes	3
Amphipods	2
Pagurids	1
Other organisms	7
Stomachs empty	33

(just over 26% of the 116 fish examined) and copepod remains were identifiable in nearly 10% of them. But, on the whole, pelagic fish caught in these months, and also in December, can be regarded as fasting. This fasting period appears to be imposed upon the fish solely by the absence of suitable food in the upper waters at this time. On or near the sea floor where food is present they do not fast, and they break their fast afterwards at any time when opportunity offers. In samples of drift-caught mackerel in early spring, most of whose stomachs are empty or contain only minute traces of food, chiefly phytoplankton, it is not unusual to find an occasional individual whose stomach is packed tightly with small pelagic fish—generally *Maurolicus pennanti*, which occur in small and localized shoals.

Bullen (1912, p. 394) is therefore correct in stating that although mackerel obtain the smaller organisms of their diet by 'filtration' the larger ones are captured by 'selective feeding'. Selective feeding has been confirmed by Damant (1921, p. 42) by direct observation in the sea. In aquarium tanks of this laboratory mackerel are fed upon fragments of squid or other suitable food which they swallow as it sinks through the water by very obvious 'visual selection'. Bullen was in error, however, in thinking (1912, p. 403) that 'when feeding upon the minor forms of the plankton mackerel are incapable of assimilating other

larger prey'. The phytoplankton present in the stomachs of pelagic mackerel in early spring can have been obtained only by filtering. It is equally certain that active fishes such as *M. pennanti*, several inches in length, must have been captured by Bullen's 'selective feeding' method. There can be little doubt that mackerel obtain their food by the most profitable method depending upon the size and kind of food organisms available to them; and that, at any time of the year and wherever they may be, they fast only if there is nothing for them to feed on.

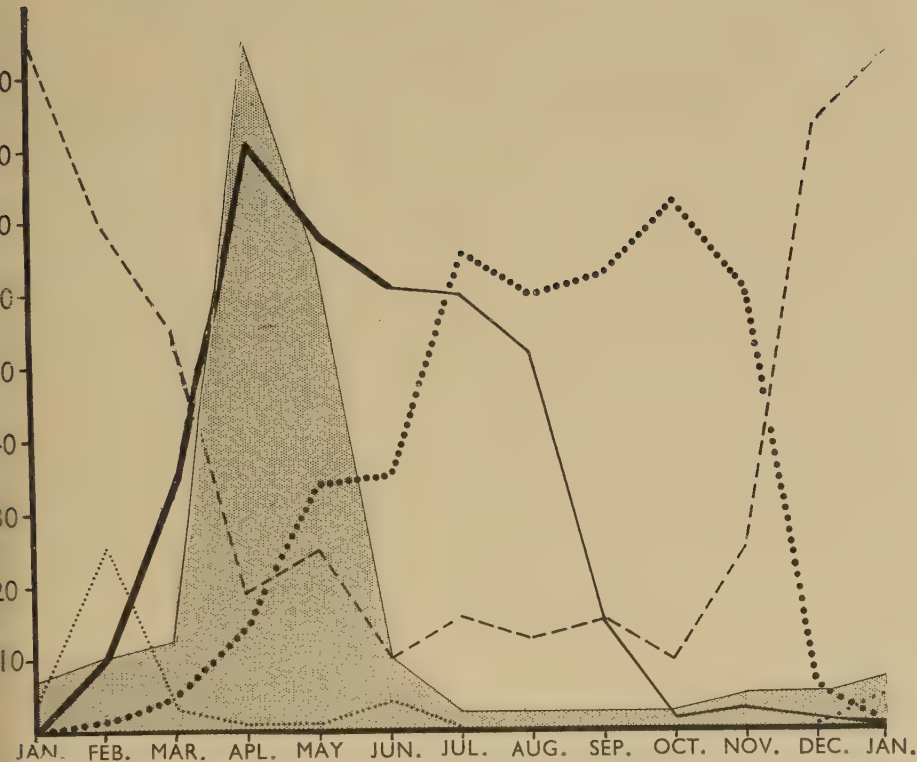
Most pelagic mackerel moving in an off-shore direction in the south-western area in the early months of the year are on migration to the spawning ground. In order to get there they leave the lower levels, where a certain amount of suitable food is available to them, for the upper layers where for a time there is practically none. The catadromous spring migration to the spawning areas is undertaken, therefore, irrespective of the presence or absence of food either at the beginning of the journey or on the way. Nevertheless, the migrating fish will at all times feed greedily if they can.

During March there is a rapid increase in the number of stomachs of pelagic mackerel containing food material—mainly copepods—and in the total quantity of food in each stomach. By the end of the month, and all through April and May, the fish feed predominantly on copepods, their stomachs being packed to bursting with these crustacea known to fisherman as 'red feed'. Although copepods predominate in the diet of the mackerel at this time a wide range of other planktonic organisms are also eaten. By about June yet another change takes place. Young pelagic stages of fish are now the mackerels' chief food, particularly *Clupea* spp., *Ammodytes* spp., and *Onos* spp. Considerable numbers of the larger crustacea also form part of the diet at this season and throughout the whole time that the fish are in shallow coastwise waters—euphausiids, mysids, the larger larvae of decapod crustacea such as *Corystes* and *Porcellana*, and even occasional pandalids, hippolytids, crangonids and similar organisms.

It will be seen (Fig. 5) that the fasting period is December—March which coincides with minimal plankton occurrence. When plankton becomes abundant the mackerel feed voraciously upon it, and continue to do so all the time that they are in off-shore waters. The change over to a predominantly fish diet, augmented with certain larger Crustacea, takes place when the mackerel have arrived back in inshore waters on their return from the spawning grounds.

FISHERMEN'S SIGNS

When fishing for mackerel, especially in the Newlyn deep-sea fishery, the fishermen are influenced greatly in their choice of position for 'shooting' their nets by what are commonly known as 'fishermen's signs'. Large congregations of birds, especially diving gannets, are looked upon as good indications of the



Text-fig. 5. Diagram illustrating the changes in mackerel stomach contents in the course of one full year. The percentage of stomachs containing the chief types of food are shown thus:, phytoplankton; —, planktonic crustacea, mainly copepods; —, non-planktonic crustacea, i.e. crangonids, pandalids, etc.; •••, fish; - - -, empty stomachs. The contents over a whole month are recorded as for the mid-point of that month. Height of the stippled area indicates, in miles, on the same ordinate, the mean distance from land at which the mackerel examined were caught in each month.

presence of fish in worthwhile numbers. Even more reliance is placed upon the colour of the water. This has already been remarked upon by Bullen (1908, p. 287) who recognized five different kinds:

- (i) Stinking water—water of a dull leaden colour having a recognizable and distinctly unpleasant smell.
- (ii) Grey water—water similar in colour to the above but lacking the smell.
- (iii) Blue water—very clear and transparent.
- (iv) Green water—differing from blue water only in colour.
- (v) Yellow water—turbid water of a distinctly yellow tint.

According to Bullen best catches of mackerel at that time (1906 and 1907) were generally, though not invariably, to be had in yellow water,¹ followed by

¹ This seems to have been first remarked upon by Pliny—quoted by D'Arcy Thompson (1947, p. 244)—who says: '*scombri quibus est in aqua sulphureus color.*'

the others in the order reverse of that given, each providing progressively poorer prospects down to the 'stinking water' in which mackerel are said never to occur.

Present-day fishermen agree that in yellow water¹ by far the best prospects of good catches are still to be had. Green water, according to their spoken testimony, comes next, but there is no unanimity of opinion about any other kinds except stinking water which, they all agree, is worst of all but fortunately is seldom encountered on the mackerel grounds.

In order to obtain more precise information on these and other points, ten selected drifters in the years 1937-1940 inclusive, were provided with special log-books in which they recorded exhaustive details of all their catches.

In recording the colour of the water in which they shot their nets the skippers were left free to use their own descriptions. For the purpose of tabulation all waters for which the term 'yellow' or 'yellowish' e.g. 'yellowish green', are used have been grouped together as 'yellow water'. All other shades of green e.g. 'light green', 'dark green', 'pale green', 'grass green' and the like have been grouped together as 'green'. The various 'blues' have been similarly treated. All other waters, e.g. 'slate', 'grey', 'paraffin oil', 'black', etc., have been grouped together under the general heading of 'other colours'. No stinking water is recorded in any of the log-books.

In the years under survey yellow waters were not very plentiful. They were encountered by log-book drifters only six times in 1937, eight times in 1938, and thirteen times in 1940. No yellow water was found by any of them in 1939.

It will be seen from Table VI that out of the total number of 27 shots made in yellow water during those four years no less than 21 (77·8%) yielded catches of over 10,000 fish, the average number per haul being 18,300.² Several catches of over 29,000 fish were made. In green water only 13·4% of the 918 catches consisted of more than 10,000 fish. In blue water, out of 183 catches only 1 had over 10,000 fish. The catches in other waters were poorer still.

It is quite clear from these log-book records that yellow water, when present, offers by far the best prospects of obtaining good catches. Yellow water is, unfortunately for the fishermen, not very plentiful, and in some years, as in 1939, may not occur at all.

Bullen (1908, p. 289) endeavoured by direct investigation to correlate the different kinds of water with the plankton present in it. Stinking water he found to be rich in phytoplankton and poor in zooplankton, but he was unable to offer any explanation of the reputed objectionable smell which he was himself unable to detect. He gave it as his opinion, though, that such an odour, if it did exist and could in fact be detected by fishermen, 'did not arise from the condition of plankton'. Long before Bullen's investigations, however, Percy (1885, p. 399), working near Shetland, had shown quite conclusively not

¹ Described by some Cornish fishermen as 'cow-dung water'.

² To the nearest hundred.

only that herrings avoid stinking water but that the odours were correlated with the presence of *Rhizosolenia shrubsolei* and *Thalassiosira nordenskioldii* with which the herring nets sometimes became so heavily coated that little slimy heaps of those organisms were formed on the deck as the nets were hauled in.

Supporting evidence that shoaling fish such as mackerel and herring avoid water heavily populated with phytoplankton, such as the diatom *Rhizosolenia* or the flagellate *Phaeocystis*, is provided by Russell (1915, p. 30) for mackerel, and by Savage & Hardy (1935) for herring. Although, therefore, stinking water has not been reported in the course of these investigations there appears to be no doubt that when it does occur poor fishing must be expected in it.

TABLE VI. CATCHES IN DIFFERENT TYPES OF WATER

Colour of water	Year	No. of shots	No. of shots having over 10,000 fish	Percentage of shots having over 10,000 fish	Average no. of fish per haul (to nearest hundred)
Yellow	1937	6	3	No yellow water	18,300
	1938	8	5		
	1939				
	1940	13	13		
		27	21		
Green	1937	230	42	77.8	5,300
	1938	327	56		
	1939	247	30		
	1940	114	5		
		918	133		
Blue	1937	88	0	13.4	2,600
	1938	25	1		
	1939	31	0		
	1940	39	0		
		183	1		
Other colours	1937	18	0	0.6	2,000
	1938	38	0		
	1939	34	0		
	1940	32	0		
		122	0		

In all other waters examined by him Bullen found zooplankton to be more plentiful than in stinking water, with phytoplankton also often present as well. In yellow water he found that phytoplankton was 'entirely absent' and that the zooplankton was confined almost entirely to three or four principal forms of which *Calanus finmarchicus* and *Pseudocalanus elongatus* were the most important.

Unfortunately, Bullen's data enable him to put forward only tentative explanations of the causes which give rise to the yellow colour and why, on the whole, yellow water is most likely to provide good catches. He quotes the 'somewhat conflicting opinions expressed by fishermen' to the effect that the coloration is due either to the presence of excrement arising from densely shoaling fish or to the abundant copepod 'feed' and adds that evidence provided by examination of certain plankton samples supports the latter view.

During the present investigations some of the skippers provided with log-books agreed also to work small townets and collect plankton samples from each position in which they shot their drift nets. They were all issued with exactly similar gear and given precise instructions for using it in such a way as to obtain reasonably comparable quantitative results. In spite of this the samples so obtained could not at first be relied upon from a quantitative point of view.

Nevertheless, their collection was continued and in due course many of the difficulties which vitiated their comparability were overcome so that some deductions could reasonably be drawn from them. These improvements arose in part because the skippers themselves found that, though by no means an infallible guide, their best catches of mackerel were generally obtained where the townet samples consisted of typical 'mackerel feed'—i.e. copepods in reasonable abundance—and they gradually learned to use the townets by standard methods for standard times in order to obtain comparable catches for their own information. It is therefore significant that, after the townets had been in use by selected skippers for one season, other skippers who at first would have nothing to do with them, asked, as a favour, to be issued with townets for their own use.

Examination of 300 samples retained as reliable, in association with the log-book records, support Bullen's finding that plankton catches in yellow water and light green water generally consisted almost entirely of copepods—chiefly *Pseudocalanus elongatus* and *Calanus finmarchicus*, with the former usually predominating both in numbers and in bulk. The largest samples of copepods also came from those two waters. These were preserved in formalin (5%) and having survived the war period have now been re-examined after an interval of more than ten years. In that time the preserving fluid in some of the jars containing copepods almost unmixed with other organisms such as *Limacina*, has acquired a yellow colour closely resembling that of the yellow waters on the fishing grounds. Certain yellow carotinoid substances from the copepods have gone into solution in the preservative fluid.

For some reason not understood, not all the copepod samples have liberated these yellow pigments into solution; but such samples, transferred into acetone, give the same tinge and depth of colour in a few months. There seems to be little doubt, therefore, that the underlying primary cause of the yellow coloration in the sea is the presence of copepods in concentrations so dense that their body pigments impart colour to the water. Such coloration will of course be augmented by their excreta in which the same pigments are present. Observation has also shown that the 'somewhat conflicting opinions expressed by fishermen' as quoted by Bullen (1908, p. 291) are probably not conflicting at all, and that the excrement produced by densely shoaling mackerel is also a contributory factor. Faecal matter expressed from mackerel is, in fact, generally of a yellowish or pinkish yellow colour. Mackerel, like most fish, tend to congregate

in greatest numbers where their most acceptable food organisms are in greatest abundance (Herdman, 1913, p. 33). Both the fish themselves and their faecal matter will therefore be most plentiful in water already tinted by copepods and the effect of this will be to strengthen the yellow coloration.

In normal circumstances the distribution of copepods in high concentrations is characterized by its 'patchiness'; so also, in consequence, is the distribution of 'yellow water'. In years of unusual copepod abundance there will be an increase of yellow water in the form of more numerous patches, many of which will also cover greater areas. Since mackerel congregate in the yellow patches, the more numerous those patches are in any year and the greater their extent, the more favourable are the chances of their being found and fished in, with consequent benefit to the commercial fishery. In years of copepod scarcity the opposite will be true. This is in complete agreement with Allen's generalization (1909, pp. 396-97) that the catches of mackerel in May in the Newlyn deep-sea fishery are to some extent affected by the amount of sunshine in the same region during the previous February and March. This effect upon catches is an indirect and very interesting one. The phytoplankton crop depends, to some extent, upon the amount and intensity of sunlight in those early months. The abundance or scarcity of copepods is in turn partly dependent upon the magnitude of the phytoplankton crop upon which they chiefly feed. Copepod concentrations, being patchy in their distribution, cause mackerel to congregate in them, and those patches can be identified by the appearance of the water. *The effect of suitable amounts of sunshine in February and March is therefore to increase the number and size of the patches of sea in which good fishing is likely.* Obviously there must be a limit to this effect; for if, in any year, the conditions were so favourable that the greater part of the whole area consisted of yellow water rich in copepods there would be no localized concentrations of mackerel and therefore no improvement in the catches. Unfortunately, Bullen's statement with regard to zooplankton and the abundance of mackerel has for a very long time created a wrong impression. He states that 'the abundance or paucity of zooplankton during a certain number of years (1903-07) appears to be correlated with the greater or less abundance of mackerel'. It must clearly be understood that abundance of zooplankton cannot possibly increase the population of adult mackerel in the year in which it occurs. It is the 'catchability' of the mackerel already in existence that is affected and which may be reflected in the commercial catches.

SUMMARY

Of the three mackerel fisheries that formerly existed in the south-west of England, only one, the Newlyn deep-sea fishery, now remains active. The fishing grounds worked by this fishery lie in the Celtic Sea as much as 100 miles to the westward of the Scilly Islands when the season opens in March,

but the distance off becomes progressively less as the season advances until, in June, when it finishes, the participating vessels are fishing close by the land. At all times best fishing is obtained on the periphery of the areas of chief spawning intensity.

The spawning season in the Celtic Sea is a very protracted one because (a) the fish do not all ripen and spawn simultaneously due to (i) the divergent conditions, especially of temperature, in which different groups spend the winter, and (ii) the different lengths of the migratory journeys they must make to reach the common spawning area; (b) in each individual female the eggs mature in successive batches that are shed one after the other over an extended period, the duration of which is not precisely known.

In the early months of the year pelagic mackerel are often found to be fasting. This is due simply to absence of suitable food in their environment at that time. The fish will always feed when food is available.

As a general rule most mackerel are caught in patches of 'yellow' water, the colour of which is caused chiefly by localized concentrations of copepods to which the fish are attracted for feeding. Copepod abundance at the height of the fishing season must be to some extent affected—indirectly through the phytoplankton—by the amount of sunshine earlier in the season. This explains Allen's correlation between early spring sunshine and commercial catches of mackerel in late spring and early summer.

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APPENDIX I

LANDINGS AT NEWLYN BY LOCAL CRAFT (SAIL AND MOTOR) AND BY STEAM
DRIFTERS IN THE YEARS 1906-38 INCLUSIVE (WAR YEARS EXCEPTED)

Year	Local craft			Steam drifters		
	No. of landings	Total quantity in cwt.	Mean weight per landing (cwt.)	No. of landings	Total quantity in cwt.	Mean weight per landing (cwt.)
1906	2159	46265	21	1850	62551	34
1907	2190	60121	28	2962	195565	66
1908	2709	36950	15	2944	112452	38
1909	1878	27549	17	2423	112189	46
1910	1476	31757	22	2281	124122	54
1911	1581	15871	10	2156	97185	45
1912	1255	13761	11	1572	65482	42
1913	806	10419	13	1537	56176	36
1919	786	15200	19	1311	84078	64
1920	1111	16470	15	2162	112683	52
1921	1721	21932	13	1963	116931	60
1922	1824	18280	10	2185	90555	41
1923	1036	20865	20	2249	106237	47
1924	750	14613	19	2182	117540	54
1925	430	4859	11	2412	122150	51
1926	290	4441	15	1888	102390	54
1927	559	3890	7	1707	58739	34
1928	273	2924	10	1301	58827	45
1929	387	983	3	1079	43670	40
1930	173	411	2	1223	43205	35
1931	77	112	1	925	50513	55
1932	202	525	3	1014	48119	47
1933	950	2321	2	1133	51223	45
1934	988	2912	3	905	55400	69
1935	694	3002	4	856	58885	69
1936	696	4547	7	777	57177	74
1937	1131	4274	4	643	40765	63
1938	935	5134	5	641	50207	78

APPENDIX II

DIFFERENCES IN TEMPERATURE IN FEBRUARY OF SEVERAL
EUROPEAN WATERS IN WHICH MACKEREL LIVE

By L. H. N. Cooper, D.Sc., F.R.I.C.

In the course of these investigations into the life history of the mackerel, the question arose whether differences in temperature of the water occurred at the time of the winter minimum between, on the one hand, the Hurd Deep, and on the other, the waters south and south-west of Ireland and near the Viking Bank west of Norway.

Hurd Deep Observations

Two lines of regular surface observations cross the Hurd Deep. These lines are worked at frequent intervals by merchant ships on shuttle service between Southampton and St Malo and between Plymouth and Guernsey. No doubt there is some uncertainty in these observations, as in all surface observations from merchant ships. Down to the level of the bottom of the English Channel vertical mixing is almost certainly thorough. We have no knowledge as to how thorough it is within the trench of the Hurd Deep.

Throughout the whole period of the Irish investigations a station was regularly worked on the Southampton—St Malo line over the eastern end of the Hurd Deep at $49^{\circ} 54' \text{ N.}, 2^{\circ} 00' \text{ W.}$ Occasionally this point was omitted, but the adjacent position $50^{\circ} 03' \text{ N.}, 1^{\circ} 55' \text{ W.}$ differs hardly at all in temperature and on a few occasions has been used instead.

The Plymouth-Guernsey line was started in 1926 and subsequently was worked rather more frequently than the eastern line.

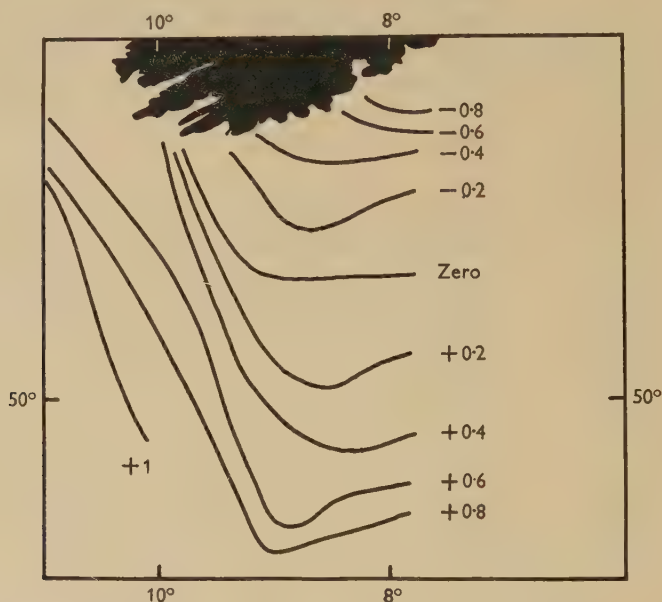
All data between the last January observation and 10 March have been abstracted from the *Bulletin Hydrographique* and, when necessary, graphed. The temperatures at each station about 1 and 19 February and 10 March were interpolated and the differences between the two stations evaluated. In general, the western station was the warmer, and for the eight years 1926–33, the position $49^{\circ} 30' \text{ N.}, 3^{\circ} 02' \text{ W.}$ was on an average 0.4° C. warmer than the position $49^{\circ} 54' \text{ N.}, 2^{\circ} 00' \text{ W.}$

It is clear that a small temperature gradient along the length of the Hurd Deep is usual, and that the easternmost station for which most data is available lies in February over the coldest part of the trench.

Observations South of Ireland

Serial temperature observations in the Irish area have been frequently taken in February and May, but in the other winter months there are few data. The

cruises were worked between 20 and 22 January in 1921 and sometime between 2 February and 10 March in the other years. In each year the mid-point in time of the Irish cruise was taken and the temperature at that time at each of the Hurd Deep positions estimated by interpolation. In the years 1926–33 the temperature of the eastern half of the Hurd Deep has been taken as the mean of these. In 1921–25, the temperatures at the easternmost position, $49^{\circ} 54' \text{ N.}$, $2^{\circ} 00' \text{ W.}$, have been increased by the mean correction, 0.2° C. , to make them comparable with the later years.



Text-fig. 6. Differences in February temperatures between the waters south and south-west of Ireland and those at the Hurd Deep in the English Channel. Lines of equal difference—positive warmer than the Hurd Deep; negative colder than the Hurd Deep. Years 1921–33.

These Hurd Deep temperatures provide the basis line for the subsequent calculations. This temperature was subtracted from each separate Irish observation between 1921 and 1933 to give a table of differences. The mean difference at each station was then evaluated and is plotted in Text-fig. 6. Lines of equal differences were then drawn which show that the inshore water south of County Cork was colder than the Hurd Deep, and that the water south of $50^{\circ} 40' \text{ N.}$, and west of $09^{\circ} 00' \text{ W.}$ was warmer. The surface water above the continental slope was about 1° C. warmer.

Quite clearly the year 1929 was peculiar and so has been omitted from these calculations. Air temperatures at Scilly and Valencia were normal, whereas at Guernsey in February they were 2.7° below average. Consequently, the water

over the Hurd Deep was 1.5°C . colder than the 'normal differences' for the other ten years would lead one to expect. This story concerns surface temperatures.

Bottom temperatures were also needed. The Hurd Deep surface temperatures apply to the whole water column at least down to the depth of the bottom of the English Channel adjacent to the Deep.

In the Irish area the water was almost always isothermal down to at least 120 m. Only a few stations deeper than 120 m. had been worked, namely positions *R*, *S*, *T*, *PP*, *QQ*, *RR*, and *SS* all west of $9^{\circ} 55' \text{W.}$, and these only in 1927, 1929 and 1932. The year 1929 has already been stated to be exceptional and it is better to use only the years 1927 and 1932 for estimating mean conditions. In these years the mean temperatures along the 150 and 200 m. contours of the shelf was about 0.9°C . higher than the temperature at the Hurd Deep. The Hurd Deep temperatures were reached at station *SS* ($50^{\circ} 34' \text{N.}$, $11^{\circ} 17' \text{W.}$) at a depth of 500 m. in 1932 and at 800 m. in 1927. In the probably exceptional year 1929, the water at the 200 m. contour was $2.5\text{--}2.8^{\circ}\text{C}$. warmer than at the Hurd Deep. Even at 986 m. the water was still 0.7°C . warmer.

TABLE VII

Date	Irish code letter	Position	Depth (m.)	Temp. ($^{\circ}\text{C.}$)
10. iii. 49	<i>D</i>	$50^{\circ} 36' \text{N.}$, $8^{\circ} 04' \text{W.}$ Labadie Bank	5	9.97
			25	10.00
			60	10.00
			70	—
9. iii. 49	<i>F</i>	<i>Sounding</i> $49^{\circ} 50' \text{N.}$, $8^{\circ} 00' \text{W.}$	5	10.30
			50	10.30
			125 ¹	10.30
			<i>Sounding</i> 123	—

¹ Wire angle $>45^{\circ}$; true depth much less than metres of wire out.

If high temperature is a factor favouring early spawning of the mackerel, those in the Celtic Sea south of $50^{\circ} 40' \text{N.}$ and west of $09^{\circ} 00' \text{W.}$ should in most years spawn earlier than those near the Hurd Deep.

The Winter of 1949 in Waters South of Ireland

Steven reported (3 March 1949) that the mackerel in the area south of Ireland had started spawning several weeks earlier than normal. Since at Plymouth the winter had been remarkably mild, it seemed likely that high temperatures of the water to the westward might have been associated with the early spawning. The opportunity occurred to obtain temperatures on 9–10 March along the meridian $8^{\circ} 00' \text{W.}$ (Table VII).

Suitable comparable temperatures had been obtained by the Irish Fisheries Service in the years 1921–22, 1924–34 and 1938, whilst surface observations are available for other years. In 1937 water as warm was present in the area of stations *D* and *F* between mid-February and mid-March, but was evidently

a short-lived intrusion into a part only of the area south of Ireland. Over the whole area for the whole of the winter, the season 1936-37 was evidently markedly colder than 1948-49. Apart from this doubtful year, it is necessary to go back to 1921 to find a similar one; even that year certainly was not warmer.

It is therefore not unreasonable tentatively to correlate the abnormally early spawning of mackerel in February and March 1949 with the notably high water temperatures.

Observations on the Western Declivity of the Norwegian Channel

During winter mackerel congregate along the western declivity of the Norwegian Channel or northern extension of the Skagerrak in the latitudes of

TABLE VIII

Depth (m.)	Deficiency in temperature (° C.)	
	7. i. 37	27. i. 37
100	2.4	2.1
125	2.4	2.1
150	2.5	2.0
200	2.8	2.0
250	3.3	2.0
300	3.7	2.0

TABLE IX

Depth (m.)	Deficiency in temperature (° C.)	
	3. ii. 37	
100	2.7	
125	2.4	
150	2.7	
200	2.8	

the Orkney and Shetland Islands (p. 564). In these waters a number of hydrographic stations have been worked by the Norwegian research vessels *Johann Hjort* and *Armauer Hansen* in January or February. The suitable stations worked there in 1938 and 1939 find no counterpart in simultaneous Hurd Deep observations.

In 1937 on 7 and 27 January, on the parallel of latitude 60° 46' N., the temperatures of the bottom water bathing the western declivity of the Channel were lower than the Hurd Deep mean temperatures on the same date by more than 2° C. (Table VIII).

On the parallel 59° 17' N., on 3 February 1937, the corresponding values were as shown in Table IX.

In 1937, mackerel in these waters were subjected to temperatures about 2.5° C. lower than at the Hurd Deep.

February 1930 seems to have provided an unusually small difference in temperatures, whereas January 1931 was more 'normal' (Table X). The parallel of latitude worked in both years was 60° 08'.8N.

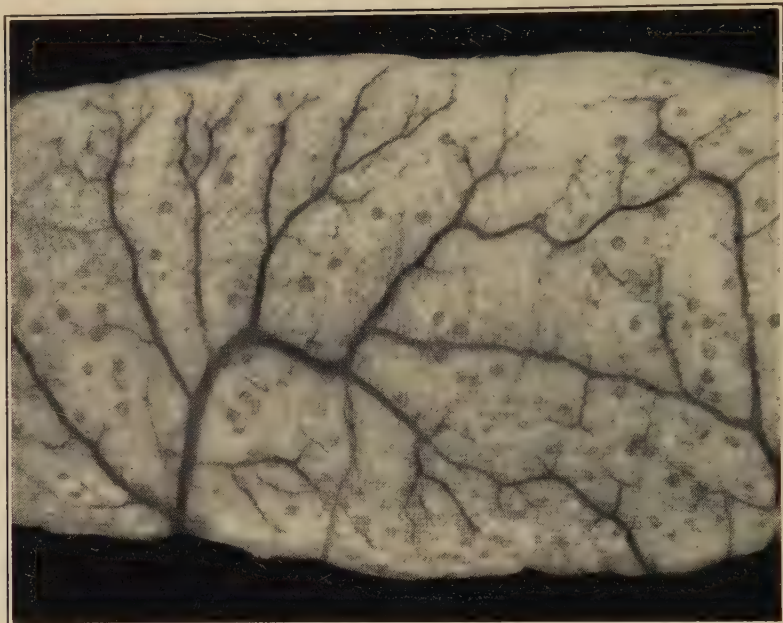


Fig. 1.

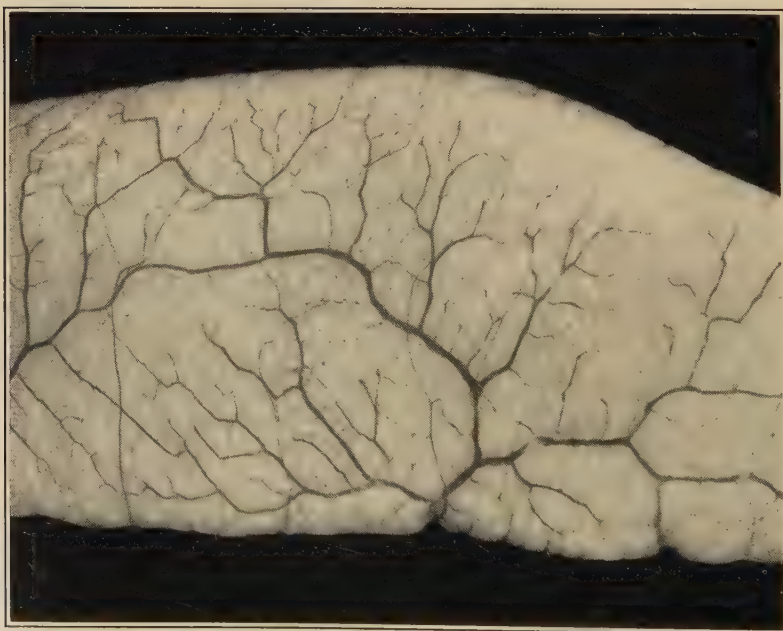


Fig. 2.

The year 1938 probably provided differences similar to 1931 and 1937.

In general we may say that the western edge of the Norwegian Channel provides temperatures 2-3° C. lower than the Hurd Deep, so that if temperature

TABLE X

Depth (m.)	Deficiency in temperature (° C.)	
	27. ii. 30	29. i. 31
100	0.3	1.9
125	0.5	2.3
150	0.5	2.0
200	0.6	2.3

controls the time of spawning, the lag in the more northern waters should be considerable.

EXPLANATION OF PLATE I

Mackerel ovary in two phases. Fig. 1, the 'plum-pudding' stage, in which the widely scattered ripe eggs appear as dark spots. Fig. 2, an ovary with ripe eggs which are not visible externally but are to be found in the lumen.

THE LARVA OF A DIDEMNID ASCIDIAN, WITH NOTES ON THE STRUCTURE OF THE COLONY AND THE ADULT

By R. H. Millar

From the Marine Station, Millport

(Text-fig. 1)

There are few adequate descriptions of British members of the ascidian family Didemnidae and little attention has been given to the larvae. In the autumn of 1947 a didemnid was collected from the intertidal zone in the Menai Strait, North Wales. This ascidian agrees superficially with *Leptoclinum maculosum* Edwards, as figured by Milne Edwards (1842) and by Alder & Hancock (1905–1912), although differing somewhat from the diagnosis of *Didemnum maculosum* (Edwards) given by Harant & Vernières (1933). It is closer anatomically to the *D. fulgens* (Edwards) of Harant & Vernières, but differs in colour. In most features the colony and zooid closely resemble the descriptions given by Michaelsen (1923) for his species *D. helgolandicum* Michaelsen, and it is probable that this is the species to which it should be assigned. Nevertheless, the name *D. maculosum* has been retained since it is under that name that it has probably appeared in most faunistic lists.

Until recently all accounts of didemnid larvae have described three anterior adhesive organs. This was the number given by Giard (1872) for *Diplosoma gelatinosum* Edwards, and by Lahille (1890) for *Trididemnum tenerum* Verrill and *Polysyncraton lacazei* Giard. Berrill (1947), however, has described a new species of didemnid, *Trididemnum allenii* Berrill, the larva of which has only two anterior adhesive organs, a condition not previously found in any ascidian larva.

The larva (Fig. 1A) of the colonies found in the Menai Strait resembles that of *T. allenii* in many features. The trunk is about 0.35 mm. long from the tip of the adhesive organs to the base of the tail. The sensory vesicle is prominent and contains an anterior static organ and a posterior ocellus. Four rows of stigmata in the branchial sac rudiment distinguish the larva from that of *T. allenii* which has only three rows. There are eight ectodermal ampullae in the anterior and ventral part of the trunk and, as in *T. allenii*, there are only two anterior adhesive organs, one dorsal and one ventral. The larva of *Didemnum maculosum* has therefore features in common with the larvae of most members of the family Didemnidae (four rows of stigmata), and also features in common with the larva of *Trididemnum allenii* (two anterior adhesive organs).

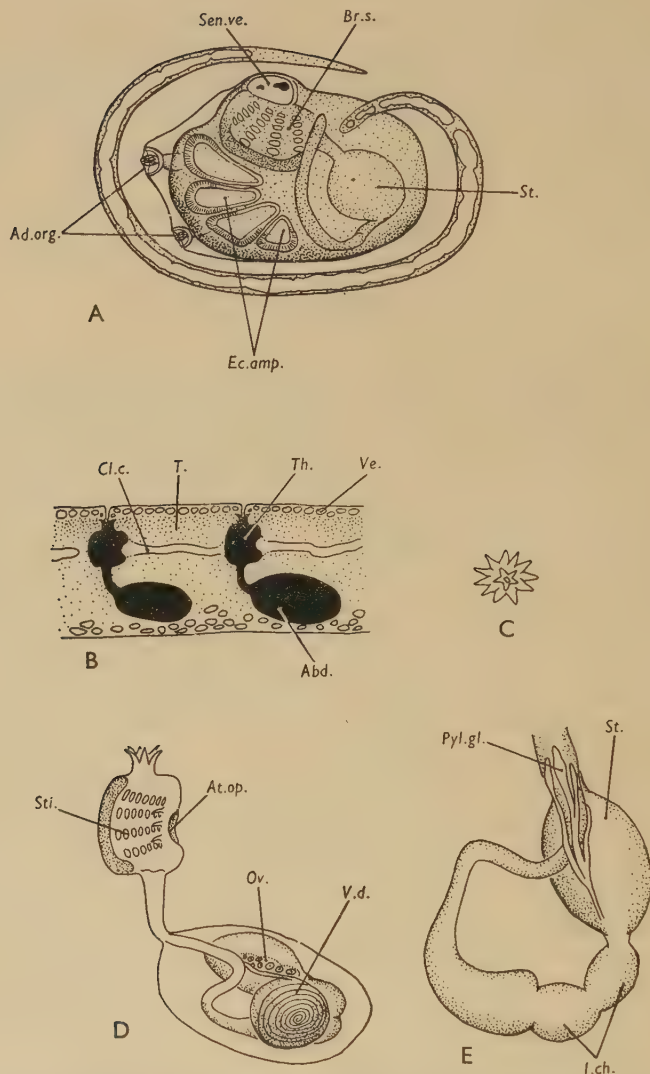


Fig. 1. *Didemnum maculosum* auctt. A, larva, seen from the left, as it appears when removed from the egg follicles. B, section through part of a colony showing the arrangement of the zooids in the common test. C, a spicule from the common test. D, zooid. E, the abdominal part of the alimentary canal.

Abd., abdomen of the zooid; Ad.org., anterior adhesive organs; At.op., atrial opening; Br.s., branchial sac; Cl.c., cloacal canal of the common test; Ec.amp., ectodermal ampullae; I.ch., first two chambers of the intestine; Ov., ovary; Pyl.gl., pyloric gland; Sen.ve., sensory vesicle; St., stomach; Sti., stigmata; T., common test of the colony; Th., thorax of the zooid; V.d., vas deferens; Ve., vesicle of the common test.

The colonies (Fig. 1B) formed large encrusting sheets about 0.5 mm. in thickness. The colour is light grey to buff, marked with streaks and spots of dark grey and purplish black. Small prominences are evenly scattered over the surface, which is also marked by deep slit-like depressions hollowed out and inhabited by the amphipod *Tritaeta gibbosa* (Bate). The dark streaks marking the colony are due to the accumulation of faecal pellets in the cloacal system of the common test, and the markings presumably become more extensive and distinct as the colony grows older. Neither oral nor atrial openings are prominent on the surface of the colony. Sections show that the most superficial part of the test is occupied by a layer of large vesicles up to 40μ in diameter. Below these is a dense mass of white calcareous spicules (Fig. 1C) which give the colony its light colour. The spicules, which also extend in smaller numbers through the lower layers of the test, are about 25μ in diameter, and have about 30 rays. A cloacal system of irregular channels exists within the common test, and into these channels open the atrial cavities of the zooids. In the lower part of the test there are often many large vesicles similar to those of the upper layers. In sectioned material a narrow channel is seen to lead from the upper surface of the test down to the oral siphon of each zooid, which lies a little below the surface. It is not certain whether this deep position of the oral siphon is an artefact produced in fixation.

A zooid is figured in Fig. 1D. The thorax lies approximately at right angles to the surface of the test. There are six pointed triangular lobes on the oral siphon and the atrial opening is a wide elliptical slit across the dorsal surface of the thorax, with no siphon. Four rows of stigmata lie on each side of the branchial sac and each row has about eight stigmata. The lateral thoracic organs are not conspicuous. A narrow stalk of moderate length joins the thorax to the abdomen, which is twice as long as the thorax and lies approximately at right angles to the lower surface of the test. The oesophagus is long, but not so long as that of *Trididemnum alleni*, and the large round stomach leads into the first of three chambers of the intestine. The first two of these chambers are small, ovoid and equal; the third is a large pear-shaped sac tapering to the narrow intestinal loop. Close beside the oesophagus lies the rectum, which is enveloped by a simple pyloric gland. The eight to nine coils of the spiral vas deferens lie on the side of the single testis, and the ovary is situated close to the stomach and part of the intestine.

The adult of this didemnid differs clearly enough from that of *T. alleni* to prevent confusion, especially in the possession of six oral lobes and four rows of stigmata. It belongs to the genus *Didemnum* and is almost certainly the species referred to as *D. maculosum* in most faunistic lists. This species, although common, does not appear to have been described previously in the larval stage, and there seems to be need of further investigation of the larvae of the family Didemnidae.

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OBSERVATIONS ON THE ABSORPTION OF RADIOACTIVE STRONTIUM AND YTTRIUM BY MARINE ALGAE

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(Text-figs. 1-10)

In the autumn of 1948, when radioactive strontium (in solution) was being used as a source of β -rays for irradiating *Gammarus*, some 'tracer' experiments were undertaken to test the degree of uptake, if any, of the 'active'¹ strontium by inanimate and living objects, including marine algae. The results obtained with algae have some special points of interest, and have confirmed the belief that the use of radioactive isotopes might become a powerful tool in advancing knowledge of the chemical exchanges between marine organisms and their environment. They are therefore described as far as they have been carried to date.

The work formed part of the investigations supported by the Atomic Energy Research Establishment² of the Ministry of Supply, who supplied the isotopes and lent special equipment, and by whose permission this account is published.

The writer gratefully acknowledges the help given in various ways by Dr J. F. Loutit and Dr G. E. Harrison, of the Radiobiological Research Unit at A.E.R.E., Harwell. Dr Harrison has been relied on for advice on the nuclear-physics aspects of the problems investigated. The pleasantest recollections are entertained of the kindness received from them and from various members of the A.E.R.E. staff during a week's visit to Harwell in December 1947.

I am particularly grateful to the Director, Mr F. S. Russell, F.R.S., for having, in the first place, afforded me the opportunity of exploring a new field, and to him and to Dr W. R. G. Atkins, F.R.S., for their constant sympathetic interest.

The work would have been impossible without the active co-operation of Dr H. W. Harvey, F.R.S., who kept me plied with practical suggestions and devised details of technique; and of Mr F. J. Warren, who effectively main-

¹ The terms 'active' and 'activity' used throughout this paper mean 'radioactive' and 'radioactivity'. Though these, as well as the expression 'decay', are well-established terms in the literature of the subject, they are retained in inverted commas for the benefit of readers who are not familiar with this field of research, and to distinguish them from the words used in the normal sense.

² Hereafter referred to as A.E.R.E.

tained the Geiger-Müller counter in working order. I am deeply grateful to them.

It was from Dr Harvey that the suggestion to investigate the larger algae originally came.

I also have pleasure in thanking Dr Mary Parke for identifications of algae, and for making up samples from the Laboratory cultures of unicellular algae, and Mr F. A. J. Armstrong for taking responsibility for disposing radioactive waste at sea.

The literature consulted on the general aspects of the subject has been mainly confined to the following books or articles:

Smyth (1945). The official White Paper on the development of atomic energy.

Lea (1946). *Actions of Radiations on Living Cells*.

Pollard & Davidson (1942, reprinted 1947). *Applied Nuclear Physics*.

Seaborg (1944). 'Table of isotopes.'

Hoag, revised by Korff (1948). *Electron and Nuclear Physics*.

Considerable delay, due to the supply situation, was experienced in securing copies of the last three mentioned.

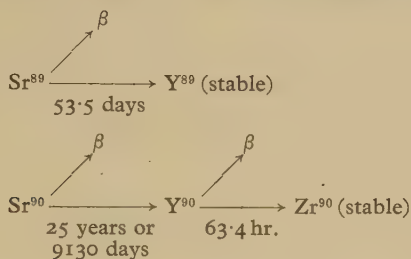
METHODS

The radioactive isotopes are here used in the role of so-called 'tracers', that is to say, they are regarded as a specially labelled component of the total amount of the element present. If, for example, interest is focused on the fate of 'active' Sr^{89} , it is not because this isotope has a peculiar chemical behaviour of its own, but because the isotope is a guide to the behaviour of the total strontium present, of which all but a negligible amount is the natural stable element. There is virtually no difference in the chemical behaviour of members of a group sharing the same Atomic Number (isotopes); and if some atoms of a new isotope are added to a previous aggregation of the element, with freedom to move, they distribute themselves at random through the aggregation. If, between its aquatic environment and an organism, the 'activity' due to Sr^{89} is found partitioned in a ratio of, say, 1 : 3, it is taken to imply that all the strontium in the system is so distributed. The wording of the title (p. 587) should thus be expanded to '... absorption of strontium and yttrium as demonstrated by changes in concentration of radioactive strontium and yttrium'.

The two essential requisites in this type of investigation are: (i) the radioactive isotope, in solution or in other suitable form; and (ii) a method of measuring the 'activity' of the experimental material, or samples of it. The manipulative technique in the application of the isotope may be very simple; on the other hand, the full analysis of the collated measurements of 'activity', including 'decay' curves of specimens, may involve much labour. This is particularly true, if, as here, more than one 'active' isotope is dealt with in the same experiment.

The Isotope Mixture

The isotope was supplied in the form of a weak solution of strontium chloride, of which all the strontium was in the form of its two 'active' isotopes, Sr^{89} and Sr^{90} . As time passes two stable 'decay' products accumulate, yttrium and zirconium, the latter very slowly. With the loss of an electron (β -ray), Sr^{89} passes direct to stable yttrium, while Sr^{90} changes first to Y^{90} , which in turn changes to zirconium. The processes are summarized as follows:



In the above formulae the periods given below the arrows are the 'half-lives' (expectation of time taken for half the original number of atoms to disintegrate, or, otherwise stated, for 'activity' to reduce to one-half). The three nuclear reactions involved proceed at very different rates, and naturally, the greater the rate of 'decay', the greater the 'activity' of the parent element. Thus, although Sr^{89} and Sr^{90} may originally be present in equal quantities, the 'activity' of the Sr^{90} will be far less—only $53.5/9130 = 0.00586$, that of the Sr^{89} . Clearly, as time passes, the ratio of the quantities of $\text{Sr}^{89} : \text{Sr}^{90}$ steadily drops, and correspondingly the ratio of their 'activities'. Eventually the 'activity' of the Sr^{90} is of comparable strength to that of the Sr^{89} , and later still accounts for virtually all the surviving 'activity'. But the 'activity' due to the Sr^{90} is, so to speak, automatically doubled through the presence of its short-lived daughter product, Y^{90} . While the daughter Y^{90} remains in equilibrium with the parent Sr^{90} , its 'activity' is identical with that of its parent; since the amount of Y^{90} 'decaying' equals the amount forming, and thus equals the amount of Sr^{90} 'decaying'. The fraction of the 'activity', in the mixture, due to yttrium may thus be appreciable, although the actual quantity present at any instant immeasurably small.

The presence of the daughter product, Y^{90} , itself a radioactive isotope, makes possible a double investigation in the experiments to be described. The absorption of yttrium can be studied in the same specimens as that of strontium.

A further physical characteristic, of which account has to be taken in making measurements, is the maximum energy of the β -rays produced by each of the reactions. Fortunately, these are not greatly dissimilar—for the rays from Sr^{89} the value is given as 1.5, for Sr^{90} it is 0.65, and for Y^{90} it is 2.2 mev. The last

have the greatest energy and are therefore the most penetrating. The screening of specimens undergoing measurement will tend to exaggerate the importance of the Y^{90} component a little.

Chemical Effects of the Isotope Solution

The actual concentrations of strontium and yttrium in the isotope solution, which was 'carrier-free' (i.e. free from stable strontium, which is mainly Sr^{88}), were so negligibly small that the chemical effects can be completely ignored. Thus, addition of some of the 'active' solution to sea water does not alter the balance of the salts originally present, or alter the pH.

Since the original solutions supplied were usually diluted with distilled water, a slight lowering of salinity was the only result. Even this effect can be obviated if desired.

Trace impurities in the original 'active' solutions were recorded as having been detected by spectrographic methods, including Ca, Ba, Al, Mg, Fe, Pb. These did not contribute to the 'activity', and were in all respects entirely negligible.

'Decay' and Daughter-product 'Recovery'

The quantity of a radioactive substance present, after an interval t , is given by the well-known logarithmic curve

$$Q_t = Q_0 e^{-\lambda t},$$

where Q_0 is the quantity at the start, and λ the specific 'decay constant' of the substance concerned. But $\lambda = \log_e 2/H = 0.693/H$, where H is the 'half-life', a constant which is more familiar than λ . Thus $Q_t = Q_0 e^{-0.693t/H}$, which simplifies to

$$Q_t = Q_0 2^{-t/H}. \quad (1)$$

This form of the equation is most convenient to use in calculating theoretical 'decay' curves, and will be adopted in this paper. A logarithmic plot gives a straight line.

The measurable 'activity' 'decays' in precisely the same way:

$$A_t = A_0 2^{-t/H}. \quad (2)$$

Suppose the solution used in an experiment contained at the start a mixture of Sr^{89} and Sr^{90} , so that the ratio of their respective 'activities' was $x : 1$. There would also be Y^{90} which had accumulated as a daughter product of Sr^{90} , with an 'activity' ratio of 1. The triple ratio is thus $x : 1 : 1$.

After an interval of t days, the respective 'activities' have become

$$x 2^{-t/53.5} : 2^{-t/9130} : 2^{-t/9130}. \quad (3)$$

For a period of a few months the change in the last two values is negligible for most purposes, so that the values simplify to

$$x 2^{-t/53.5} : 1 : 1. \quad (4)$$

A general 'decay' curve for mixtures of Sr^{89} and Sr^{90} has been worked out. For any given mixture a corresponding point on the curve is found, and the predicted subsequent history of the mixture is given by following the curve from that point.¹ This curve is frequently referred to hereafter as the 'equilibrium decay curve': it is only valid if the Y^{90} remains in equilibrium with the Sr^{90} .

Under some conditions all, or part, of the yttrium formed may be removed from the solution: for example, it may be adsorbed on objects in contact with the solution. If the yttrium is removed at a constant rate a new equilibrium is established in which the 'activity' of the Y^{90} is less than that of Sr^{90} .

Supposing that yttrium has been removed, and the mixture then allowed to recover equilibrium—as might happen when a drop is removed from the yttrium-deficient solution and placed on a slide for measurement. If the specimen is measured at intervals it will be observed to *increase* in 'activity' for a time, for the rate of accumulation of Y^{90} will at first be greater than the combined 'decay'. If the 'activity' at first is

$$x : 1 : 0,$$

after an interval of t days it becomes

$$x2^{-t/53.5} : 2^{-t/9130} : \frac{9130}{9127.36} (2^{-t/9130} - 2^{-t/2.642}). \quad (5)$$

The more complex expression for Y^{90} 'activity' is sufficiently close to $(1 - 2^{-t/2.642})$ for most practical purposes. Its value increases rather rapidly from zero during the first few days, when the rate of increase of the Y^{90} is greater than the rate of decrease of all three constituents combined. After a definite interval a maximum is reached. This time is easily calculated by differentiating and equating to zero. This gives

$$\frac{9130}{9127.36} \times \frac{1}{2.642} 2^{-t/2.642} = \frac{x}{53.5} 2^{-t/53.5} + \left(\frac{1}{9130} + \frac{1}{9127.36} \right) 2^{-t/9130},$$

or, simplifying for short periods, when the last term on the right can be ignored,

$$\frac{1}{2.642} 2^{-t/2.642} = \frac{x}{53.5} 2^{-t/53.5},$$

or

$$t = 12.062 - 9.2325 \log x. \quad (6)$$

When only part of the yttrium has been lost, and if the activity ratios are at first: $x : 1 : y$ (y being < 1); then after an interval of t days it becomes

$$x2^{-t/53.5} : 2^{-t/9130} : \frac{9130}{9127.36} 2^{-t/9130} + \left[y - \frac{9130}{9127.36} \right] 2^{-t/2.642}$$

¹ Since this curve is a compound of two curves, it is not a straight line when plotted logarithmically.

The 'activity' rises to a maximum when

$$\frac{\left(\frac{9130}{9127.36} - y\right) 2^{-t/2.642}}{2.642} = \frac{x}{53.5} 2^{-t/53.5} + \left(\frac{1}{9130} + \frac{1}{9127.36}\right) 2^{-t/9130}.$$

Again, neglecting the last term, and approximating,

$$\frac{(1-y)}{2.642} 2^{-t/2.642} = \frac{x}{53.5} 2^{-t/53.5},$$

$$\text{or} \quad t = 12.062 + 9.2325 [\log(1-y) - \log x]. \quad (7)$$

Equilibrium is said to be attained when the 'activity' curve approximates to the general 'decay' curve, which depends solely on the proportion of Sr^{89} to Sr^{90} in the sample—in other words, when the term $2^{-t/2.642}$ in expression (5) has become negligible.

Many of the curves shown in the figures are seen to start with an initial rise before reaching a maximum, and then falling to meet the equilibrium 'decay' curve. This is due, as just explained, to 'yttrium recovery', the specimen being to some degree yttrium-deficient when it was first prepared.

Other curves are seen, by contrast, to start with a steep drop (Figs. 3 and 8) and grade exponentially towards the gently downward slope of the equilibrium 'decay' curve. In these the specimen starts with an *excess* of Y^{90} , and nearly always contains an object or part of an object which has a special tendency to take up yttrium.

Clearly, by careful estimation of these departures from the equilibrium 'decay' curve, a calculation can be made of the degree to which yttrium had been removed or concentrated. The point at which the curve starts (the initial measurement), and the length of time taken to reach a maximum or attain near equilibrium provide critical data.

Composition of the Solutions Supplied

Two separate consignments of 'active' solutions have been received and used in experiments. These are referred to, for brevity, as 'the May solution' and 'the September solution'.

The 'May solution', from investigation of its 'decay' rates at various times, is estimated to have had a $\text{Sr}^{89} : \text{Sr}^{90} : \text{Y}^{90}$ ratio of

$$\begin{aligned} &39.449 : 1 : 1 \text{ on 1 April 1948} \\ &= 9.443 : 1 : 1 \text{ on 21 July} \\ &= 2.092 : 1 : 1 \text{ on 15 November.} \end{aligned}$$

The 'September solution' was similarly estimated to have given:

$$\begin{aligned} &9.78 : 1 : 1 \text{ on 23 September 1948} \\ &= 2.707 : 1 : 1 \text{ on midnight 31 December/1 January 1949} \\ &= 1.250 : 1 : 1 \text{ on midnight 1/2 March.} \end{aligned}$$

Several dilutions of these solutions have been made, usually by addition of measured volumes of distilled water to accurately measured 1.0 or 0.5 ml. portions of the original solution.

Measurement of 'Activity'

A Geiger-Müller counter, loaned by A.E.R.E., was used for measuring the 'activity' of prepared specimens. Descriptions of this excellent instrument may be found elsewhere (see Pollard & Davidson, 1942, pp. 26-30; Hoag, 1948, pp. 442-52 for the principles of construction), though doubtless much remains to be written on the subject of its occasional vagaries. It is, however, becoming a familiar object in laboratories, and can serve as an instrument of high precision.

The counter-tube was cased in a M.R.C. Castle and provided with a 'quenching' unit, which allows of precise correction for dead time. A Variac voltage control was fitted to the input of the scalar unit to ensure a steadier voltage than is supplied by the Plymouth electricity authority.

Specimens for measurement were mounted on a microscope slide. These were usually 0.05 ml. drops of a solution, carefully measured and evaporated on a warm tray. The solutions being 'activated' sea water, or at least brackish water, the evaporated drop consisted of a fine-grained crystalline patch. An optimum rate of evaporation was found which kept the crystals small and the dried patch even. Other mounts, of thin solid objects, such as pieces of the fronds of algae, or aggregates of unicellular algae, were also made. With solid objects the weight of the specimen was determined when necessary.

Of the four positions in which the tray of an M.R.C. Castle can be placed, position 1, that nearest to the counter-tube window, was used most frequently. In this position the 'efficiency' of the counter proved to be about 10.6%.¹ (A count of 100 per minute was given by 4.2×10^{-10} curies in an evaporated drop. See below.)

Measurements are obtained in terms of discharges, converted to impulses, per minute. When accurately calibrated, one recorded discharge in the counter represents one photon or particle absorbed by the counter (photons of X-rays, γ -rays, or cosmic rays; particles of α - or β -rays). The counter-tube, however, does not necessarily record all potentially available radiation—that is, particles which traverse it, or photons which have a reasonable probability of giving up their energy to it. With β -rays, with which alone we are concerned here, the capacity for absorption is quite high. Not all β -rays which impinge on the counter-tube window, however, are registered, since a fraction are absorbed in the window itself (made of aluminium foil). The conversion of 'counts' per minute into absolute terms, say total β -rays discharged by the specimen, involves various complications, but for the most part the problem can be ignored, since most of the critical results involve simply computing *ratios*

¹ In the second position the equivalent efficiency is about 3.65%.

between different readings. Results are expressed in relative terms, or related to the same arbitrary scale.

Conversion of counter readings into curie units has been made possible by A.E.R.E., who now supply a standardized solution of P^{32} (giving β -rays of 1.7 meV. maximum energy). Specimen drops have been made up of such a solution in the normal manner. To these can be assigned a definite $\mu\text{C.}$ value, subject to the correctness of the specification of the standard, the accuracy of the official value for the half-life of P^{32} (14.30 days), and within the limits of accuracy of the measured drop. It was found that an evaporated drop of 0.05 ml. volume, on a microscope slide resting on a tray in position 1 of the castle, will give a count of 100 per minute if it contains 4.2×10^{-10} curies. This is equivalent to $8.4 \times 10^{-8} \mu\text{C.}$ per ml.

In working the counter the chief necessary precaution has been to guard against minor fluctuations in the rate of counting. All counter-tubes used have exhibited these. Such fluctuations are made possible, apparently, by the fact that some particles entering the counter-tube cause two discharges, and others sometimes fail to cause any. An uneasy balance between these two opposite variations, which tend on the average to cancel each other out, but of which each may on occasion predominate, has to be carefully watched. The best safeguard is the use of a constant source of 'activity', preferably one not subject to measurable 'decay', such as a solid containing uranium. Such a constant source, made of uranium oxide, has been used continuously, and as far as possible the voltage supplied to the counter-tube has been adjusted so that it tended to give a certain constant reading (4930 per minute, uncorrected, on tray in position 1).

All readings have a standard 'dead time' correction¹ (see Kamen, 1948, p. 82), which has to be added, and a constant 'background' count has to be deducted. At Plymouth, values for the background of reasonable accuracy vary between 8.7 and 10.2 per minute, with 9.5 as a modal value. The latter figure is adopted as the routine correction.

Radioactive 'decay' proceeds essentially at random, though when it is producing impulses at the rate of several thousand a minute this fact is hard to grasp. One result is that variations in counts due to sampling follow the well-known Poisson distribution curve, for which the variance (σ^2) is conveniently equal to the mean. Supposing a specimen is measured for 30 min. during which period it has given a count, corrected for dead time, of 3600. This figure has a variance of 3600 ($\sigma = 60$), and so the value per minute, i.e. 120, has a σ of $60/30 = 2.0$. [Alternatively, $\sigma^2_{\text{mean}} = 120/30 = 4$, $\sigma_{\text{mean}} = 2$.] In practice a background value of 9.5 per minute will have to be deducted from the empirical count of 120 per minute, giving 110.5. The corresponding error must not be deducted, but added. For the σ^2 of this corrected mean is $(120 + 9.5)/30 = 4.317$, and $\sigma_{\text{mean}} = 2.07$ (or what would normally be the

¹ For the particular quenching unit used, the count corrected for 'dead time' was $N/(1 - 0.000,005N)$, where N was the actual count per minute.

error for a mean of 129.5). Similarly, the error for 30-9.5 is a function of 39.5, not of 20.5. It will thus be appreciated that when counts are low, say 60 per minute or less, and the background has to be deducted, the sampling error may be considerable.

Sampling errors have not been computed as a matter of routine, and it is not considered necessary to append them to all readings recorded here. They have, of course, been considered when critical comparison has been required. It is necessary to state that the accuracy of different measurements quoted is variable. Often time could not be spared to keep a specimen in the counter as long as might have been wished. Strongly active specimens are the more accurately measured, requiring less time for a given accuracy, and thus are to be recommended for economy of effort. A count of between 2000 and 6000 per minute should be aimed at, and the specimen given a run of at least 30 min.

Actual sampling errors are probably rather greater than the ideal theoretical, on account of that element of fluctuation in the performance of the counter-tube for which it is impossible to correct completely.

EXPERIMENTS WITH ALGAE

In the experiments to be described, of which the one now related in detail was the first, the technique was extremely simple. Sea water was 'activated' by the addition of a small volume of an 'active' solution. A measured volume was put into each of two or more similar glass vessels, usually boiling tubes. One vessel was kept as control, while into the other, or others, was placed a piece of healthy alga frond. The wet weight of the piece of frond, which varied from 1 to 5 g., was determined at some stage, usually after the water had been sampled. The mouths of the vessels were covered with a glass plate, or stoppered with cotton-wool plugs. They were stood near an artificial daylight source which was kept continuously lit. After an interval, varying between 2 and 5 days, the water in the vessel was tested by the drawing off of one or two measured drops. These were placed on a slide, evaporated, as described above (p. 593) and presented to the counter. The remainder of the experiment consisted in the investigation of changes in the 'activity' of these evaporated drops. Sometimes a second or third test was made a day or two later. Details of procedure varied on different occasions, and these will be mentioned as the account proceeds. Small improvements were continually being made, particularly in the accuracy with which the specimen drop was measured and mounted.

The standard quantity taken for each drop was 0.05 c.c., or, at first, an approximation to this. I am much indebted to Dr Harvey for adapting a 0.1 c.c. pipette in a simple but effective way, so that it could be manipulated accurately by hand. The liquid could be steadied and finally levelled by

a screw adjustment; care being taken that the glass surface remained clean, the accuracy with which the drop was ultimately measured kept within the limits of 1% either way. In the first experiment, however, there were possibilities of a considerably greater error.

The measured drop is placed in the centre of a glass slide and allowed to evaporate. The exact shape of the drop is not important, provided the area keeps within that of the window of the counter, i.e. it must not be allowed to attenuate too much in any direction. It is well for the evaporation to take place fairly quickly, say in 10 or 15 min., when the crystals of sea salt will be small. The presence of large crystals may increase the self-absorption of the specimen and give somewhat low readings. The slides should therefore be placed on a warm tray, or over a weak bunsen flame. They should be stored in a place where deliquescence in a saturated atmosphere does not occur.

For measuring the 'activity' of the specimen, the slide is placed in the chamber of the counter so that the specimen (evaporated drop) is in an exactly defined position. It is necessary, of course, that all the microscope slides used should be of the same thickness, otherwise variations, small, but important, will arise in the distance of the specimen from the window.

As soon as a specimen is prepared its 'activity' is measured, and further measurements are made at intervals subsequently. From the nature of the 'decay' characteristics of the specimen and the relation between it and the control specimen, the degree of absorption of the 'active' ions by the weed can be accurately determined. It is not necessary to examine the weed itself further, but valuable supplementary or corroborative data can be obtained by mounting a fragment of the alga, well washed, and investigating the 'decay' characteristics of any 'activity' it may have absorbed.

The method of analysing and interpreting the 'decay' characteristics of specimen drops is best explained when the results of an actual experiment have been given.

An Experiment with Fucus serratus and Rhodymenia palmata

In the first experiment, set out on 20 October 1948, four boiling tubes were taken and into each 25 ml. of sea water were measured, and to each 0.5 ml. of an 'active' solution added. [The 'active' solution was the May solution diluted $\times 114$.] Into one tube (*P*) a piece of *Rhodymenia palmata* Grev. frond, 1.4 g. in weight, was added, and the second tube (*Q*) kept it as control. Into a third tube (*R*) a piece of *Fucus serratus* L., 1.2 g. in weight, was added, and the remaining tube (*S*) kept with it as control.

It may be noticed that the control solutions are not strictly identical with those of the alga-containing tubes, since the 'active' 0.5 ml. was added to each independently, and each tube was liable to a different error in the estimation

of the 0.5 ml. added to it. Tubes *Q* and *S* were therefore 'similarly treated' as tubes *P* and *R*.

The *Rhodymenia* tube (*P*) was sampled 3 days later, on 23 October, together with its control (*Q*), and again on 27 October. Two drops were taken in each sampling (*P*_i and *P*_{ii} on 23 October; *P*_{iii} and *P*_{iv} on 27 October; *Q*_i and *Q*_{ii} on 23 October). The *Fucus* tube (*R*), with its control (*S*), was sampled on 25 October (drops *R*_i, *R*_{ii} and *S*_i, *S*_{ii}), and again on 27 October (*R*_{iii} and *R*_{iv}).

In working out the results of 'activity' measurements, the mean of each pair of drops is taken. Thus $\frac{1}{2}(P_i + P_{ii}) = Pa$; $\frac{1}{2}(P_{iii} + P_{iv}) = Pb$; $\frac{1}{2}(Q_i + Q_{ii}) = Q$, and so on. The 'activity' curves of the various specimens are given in Fig. 1 (*Rhodymenia*) and Fig. 2 (*Fucus serratus*).

A glance at the *P* and *R* curves, the positions of which would be widely separated were they placed on the same graph, shows at once that the two algae have given entirely different results. Before, however, this difference is analysed, it is necessary to consider each graph separately, and to be clear how each alga-containing tube differs from its control.

Taking tube *P* first—it is seen that on the day the sampling was made (23 October) the water in *P* shows appreciably reduced 'activity' as compared with *Q*, though not excessively less (actually 81%). During subsequent days there is some increase in the 'activity' of the control specimen, which reaches a maximum about 27 October, after which it begins to show the expected 'decay'; but there is still greater increase in the 'activity' of the specimen of alga-treated water, as shown by the steep rise in the curve *P* (actually it is *Pa* which is plotted), which does not reach a maximum before about 1 November. The difference between *P* and *Q* steadily reduces until the two values are within 5%, or less, of each other, the final mean ratio of *P/Q* being 96.05%.

As explained above, an increase in the 'activity' of a specimen shows that, when it was prepared, it was deficient in yttrium. The daughter product, Y^{90} , has been wholly or partially removed and is below equilibrium value. In the specimen itself, the amount of Y^{90} will gradually be restored to equilibrium value by the decay of Sr^{90} . The rate at which this occurs can be calculated as precisely as the accuracy of the values of the 'decay'-constants of Sr^{90} and Y^{90} permit. The greater the deficiency of yttrium, the longer is the period of 'recovery' before a maximum 'activity' is attained, and before the eventual establishment of equilibrium, when the 'decay' follows the theoretical curve determined from the ratio of Sr^{89} to Sr^{90} in the mixture.

The initial loss of 'activity' due to the removal of Y^{90} cannot exceed a certain value at a given moment, determined by the proportion of Y^{90} 'activity' out of the total, itself in turn determined by the proportion of its parent Sr^{90} . Once the 'activity' ratio of $Sr^{89} : Sr^{90}$ has been determined for a particular hour, the expected fraction of 'activity' due to Y^{90} can be worked out for any

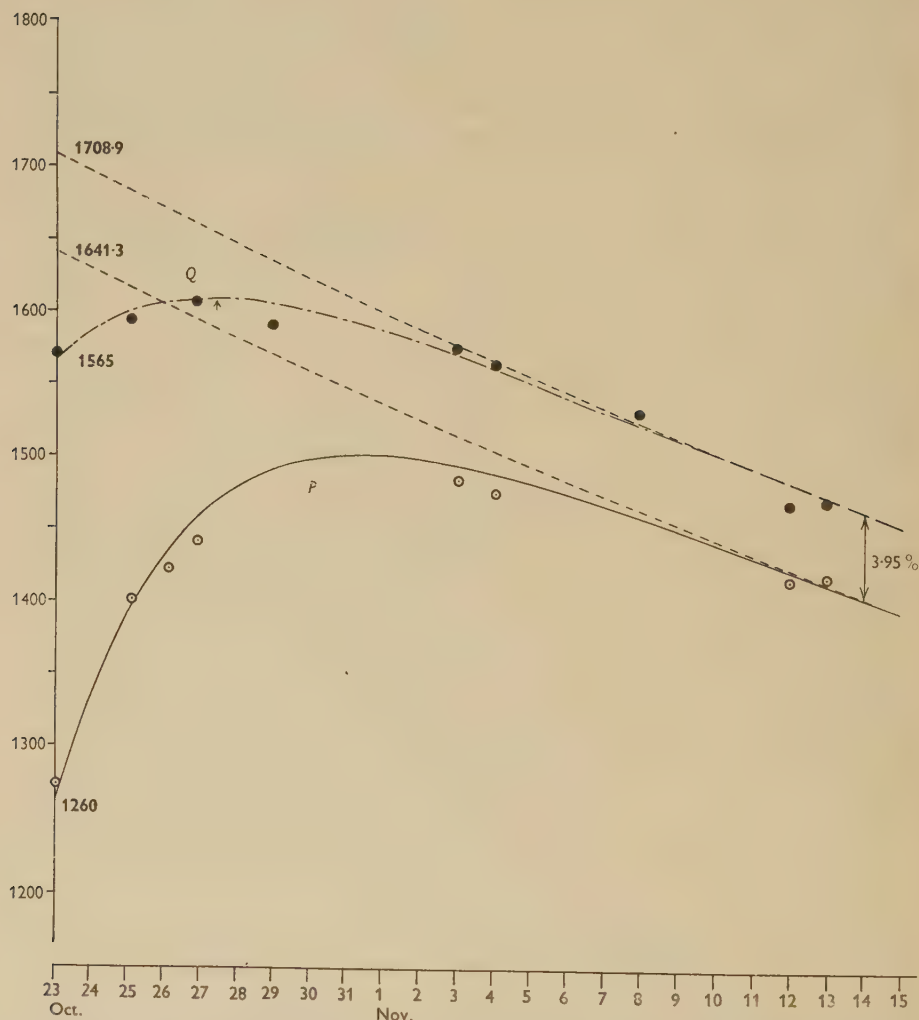


Fig. 1. 'Decay' characteristics of a specimen of 'activated' sea water (*P*) which had contained a piece of *Rhodomenia* frond; compared with a control specimen of 'activated' sea water (*Q*). Tube *P* had held 1.4 g. of alga in 25.5 ml. of sea water. Curves have been fitted to the two series of points on the assumption that the initial rise is due to recovery of an initial deficiency of Y^{90} . The close-pecked lines represent the two equilibrium 'decay' curves, to which the curves *P* and *Q* respectively tend. Activity in arbitrary units. The heavy numerals represent the estimated values of each of the curves at the isolation of the specimens on 23 October.

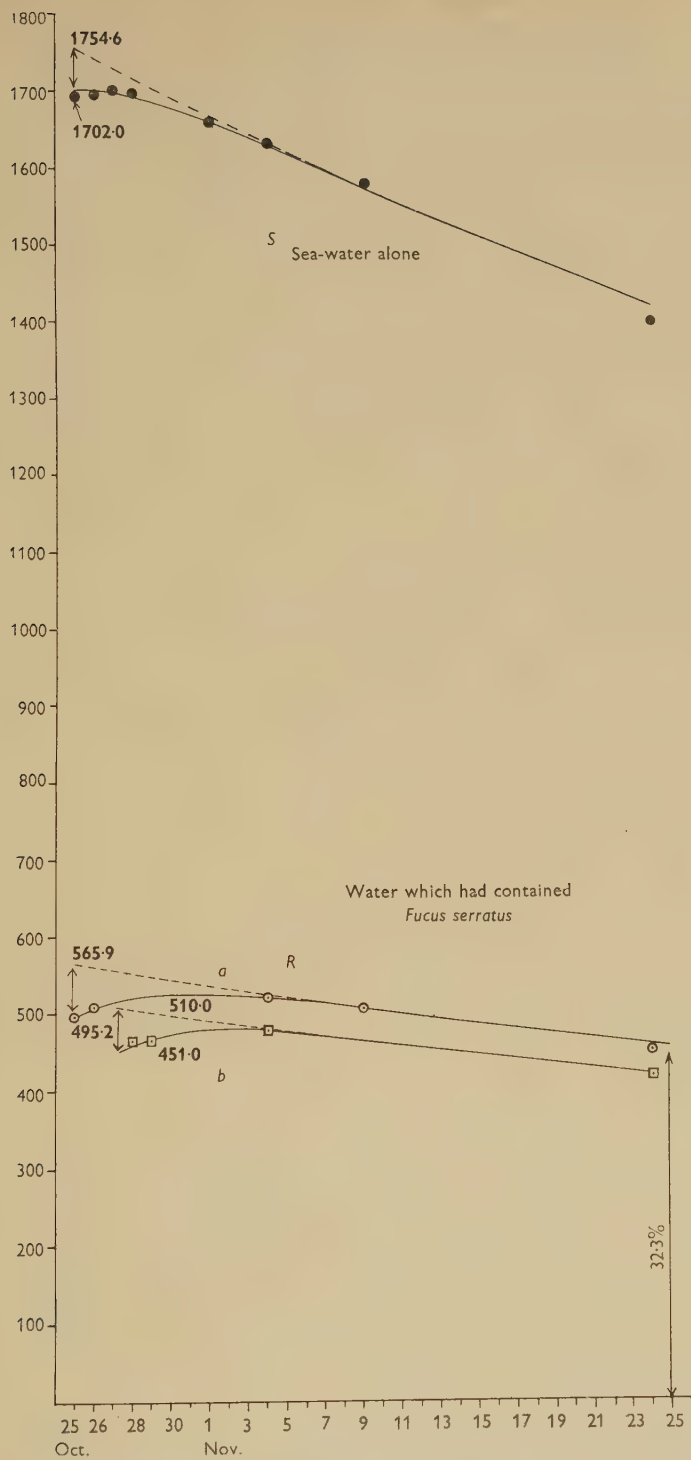


Fig. 2. Curves showing 'decay' characteristics of sea water (*R*) which had contained a piece of *Fucus serratus* frond, compared with a control specimen (*S*). Tube *R* had held 1.2 g. of *Fucus serratus* in 25.5 ml. of sea water, and two specimens (*a* and *b*) were examined from it. The lines with arrows on the left indicate the extent of the initial yttrium deficiency. Other particulars as in Fig. 1.

other moment. On 23 October this fraction would appear to have been 20.7%, or 22.5% as measured by a Geiger-Müller counter.¹

The control water (*Q*) has lost a certain fraction of Y^{90} , no doubt adsorbed on the wall of the boiling tube, which had not been subjected to stringent cleaning prior to the experiment (it is known that *Y* is liable to be adsorbed on certain types of glass). There is 'recovery' for 4 days, and equilibrium is virtually attained by 4 November.

The water which had contained *Rhodomenia* had lost considerably more of its yttrium; indeed, it had lost an amount representing all, or very nearly all, the yttrium that could have been present. The alga must therefore have taken up all, or nearly all, the 'active' yttrium which had not gone on the glass of its tube. Hence *Rhodomenia*, in some way,² differentially concentrates yttrium.

On the other hand, since the final values of *P* and *Q* are so close, there is no differential absorption of 'active' strontium. The 4% or so reduction is of the order of the amount by which the 'activated' water is diluted by the addition of 1.4 g. of 'unactivated' weed. The accuracy of this particular experiment does not allow of more precise estimates, and it can not be said whether the weed has differentially *excluded* strontium.

The value of *Pb* on 27 October was, as expected, slightly less than that of *Pa* on 23 October, and again suggested that all, or nearly all, the Y^{90} had been taken up. The 'recovery' and 'decay' of *Pb* was not studied.

Two days, therefore, is adequate for this differential absorption of Y^{90} to occur.

The results given by *Fucus serratus* are in strong contrast (Fig. 2). The control solution (*S*) gives a curve comparable with *Q*, except that it had lost rather less Y^{90} to the glass of its tube, either because this was of a different quality of glass, or a shade nearer complete cleanliness. It had virtually recovered equilibrium by 29 October. But the alga-treated solution (*R*) shows greatly reduced activity, and, unlike *P*, never recovers to the level of the control. This state of affairs deserves close attention, since it points to a substantial concentration of strontium in the *Fucus*.

Tube *R* was sampled on 25 October, giving curve *Ra*, and again on 27 October, giving curve *Rb*. Main attention was devoted to the former when the other had been found substantially to confirm it. It is instructive to consider *Ra* as a percentage of *S*. On the first day, 25 October, this percentage was 29.2. By 4 November, when both samples had nearly attained equilibrium, it has risen somewhat to 32.02, and subsequently settles to a constant value of some 32.26. This value of 32.26% represents the drop in concentration of the strontium in 25.5 ml. of water as a result of adding 1.20 g. of *Fucus serratus*.

¹ The high energy Y^{90} β -rays have a smaller absorption in the window of the counter.

² See pp. 616-18 and 620-3 for discussion of this phenomenon.

Thus, adding 1.20 g. of *Fucus* was equivalent to diluting with

$$\frac{25.5}{0.3226} - 25.5 = \frac{25.5 \times 0.6774}{0.3226} = 53.55 \text{ ml.} = 55.0 \text{ g. of sea water,}$$

or $55.0/1.20 = 45.8$ times as much by weight.

The slight rise in 'activity' apparent during the first few days in both the *Ra* and *Rb* specimens makes it clear that the water was even more deficient in yttrium than deficient in strontium. It is easy to calculate that only about 46% of the expected amount (i.e. of that in equilibrium with the Sr present) remains in the water.

To sum up at this stage, it appears from deficiencies in the sea-water medium that the *Rhodymenia* has absorbed nearly all the available 'active' yttrium, but no strontium, whereas the *Fucus serratus* has taken up part of the yttrium and a good deal of strontium as well. These deductions can be tested by direct observations on the weed itself, as will now be discussed.

A rectangular fragment of the *Rhodymenia* frond, which was found to have a wet weight of 0.012 g., was placed on a microscope slide and treated as an ordinary specimen. It had first been well rinsed in distilled water, and after mounting it had frequently been moistened with distilled water to keep it something approaching its original shape. The first counter reading, on 5 November, was 4784 per minute (Fig. 3, curve *P*). 'Decay', however, was rapid, and it was soon clear, after a few readings at regular intervals, that the rate of 'decay' was close to that of pure Y^{90} —that is with half-life between 60 and 70 hr., or tenth-life of just under 9 days. In 10 days (15 November), indeed, the reading had fallen to 398 per minute. After this the rate of 'decay' gradually eased, until, in early December, it had nearly attained the slow rate of a strontium mixture in equilibrium. By 10 December, when excess Y^{90} must have practically disappeared, a count of 42.5 per minute remained, due to strontium (including the Y^{90} in equilibrium with it). The final analysis, given in Table I, shows that, on 5 November there was (in arbitrary units of 'activity'):

4729.7 due to excess Y^{90} .

53.9 due to the Sr mixture, including the Y^{90} in equilibrium with it.

= 4743.1 due to Y^{90} , 40.5 due to $Sr^{89} + Sr^{90}$.

In other words, the *Rhodymenia* had taken up a very appreciable amount of 'activity', of which more than 99% is due to yttrium. Without pressing the significance of the actual figures too far, it is easy to see that the weed had not only concentrated available yttrium very heavily, but had, by contrast, taken up very decidedly less strontium than might have gone into it by free interchange. It may be said to have 'differentially' excluded strontium. The conclusions reached before are thus confirmed and amplified.

A piece of *Fucus serratus*, similarly treated (Fig. 3, curve *R*), clearly behaved

quite differently. This specimen, however, was not so satisfactory for prolonged study: after a week or so it had dried too far and become strongly curled at the edges. Though it was cut into pieces which could lie together more or less flattened, the original shape could never be restored, and exact results could no longer be expected from it. However, during the first week

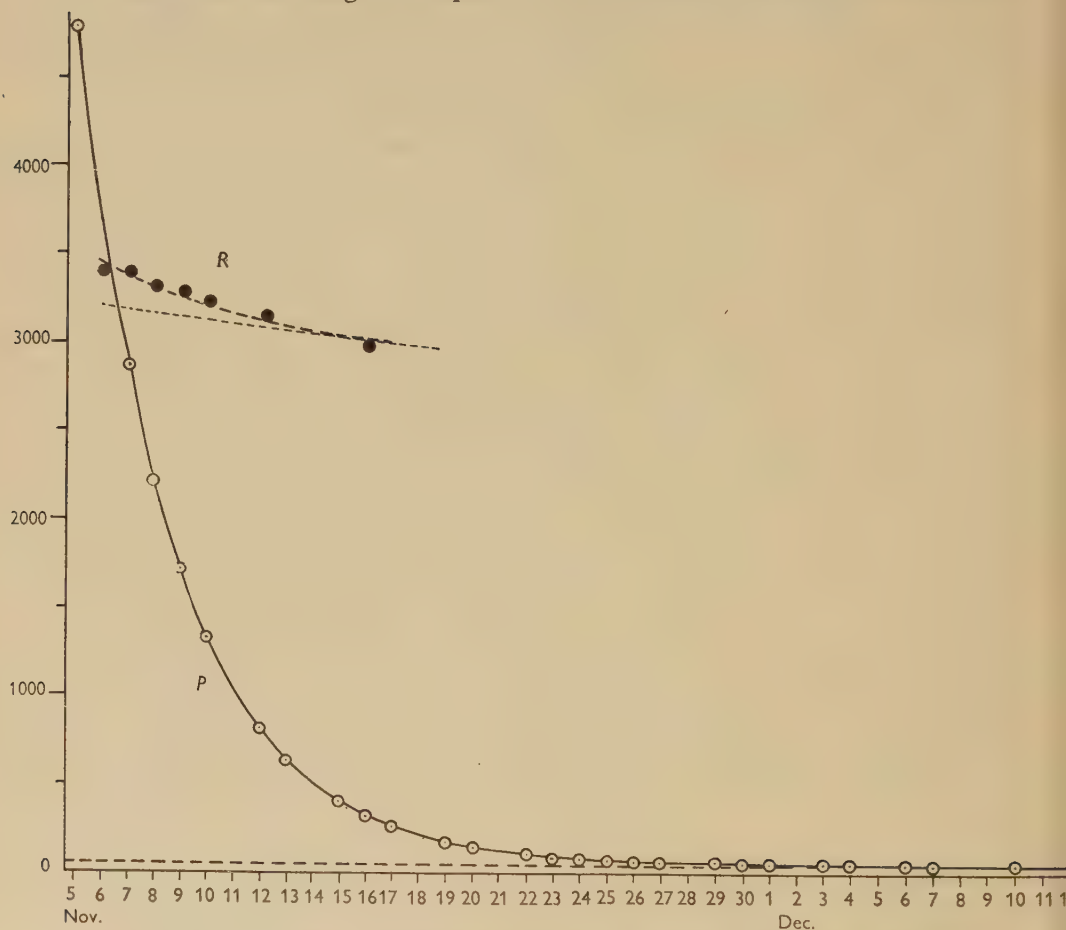


Fig. 3. 'Decay' curves of specimens of alga which had been placed in 'activated' sea water—*P*, *Rhodymenia falcata*; *R*, *Fucus serratus*. These corroborate the conclusions derived from the study of Figs. 1 and 2. *P* is seen to have acquired activity which is due almost entirely to Y^{90} . The activity of *R* is mainly due to 'active' Sr mixture, but it has a little excess Y^{90} . The units of the two curves cannot be directly compared.

or so the rate of 'decay' shows two things clearly: (i) the 'activity' must have been mainly derived from strontium, but (ii) it started with an appreciable excess¹ of Y^{90} , the 'decay' of which is apparent during the first few days.

¹ I.e. excess over the equilibrium value.

About 3208 of the original count of 3442 (on 6 November) seems to have been due to the strontium equilibrium mixture and 234 to excess Y^{90} . The partial deficiency of Y^{90} in the water has thus a counterpart of excess in the weed. Again there is corroboration of the conclusions derived from the first method.

TABLE I. 'DECAY' OF 'ACTIVATED' *RHODYMENIA* FROND (SPECIMEN *P*)

'Activity' (in arbitrary units) of a specimen mounted on 5 November and re-measured at noon on various subsequent days.

	(1) Total 'activity'	(2) Part due to Sr equilibrium mixture	(3) Part due to excess Y^{90}
5 Nov.	4783.6	53.9	4730
6	3630.2	53.5	3577
7	2869.0	53.2	2816
8	2209.0	52.8	2156
9	1713.2	52.4	1661
10	1328.8	52.1	1277
12	816.9	51.4	766.5
13	633.5	51.0	582.5
15	398.1	50.4	347.7
16	313.4	50.0	263.4
17	255.1	49.7	205.4
19	170.8	49.1	121.7
20	143.0	48.7	94.3
22	102.8	48.1	54.7
24	79.5	47.5	32.0
25	76.0	47.2	28.8
26	66.25	47.93	19.3
27	61.06	46.64	14.4
29	53.22	46.08	7.1
30	55.65	45.80	9.8
1 Dec.	49.23	45.53	3.7
3	49.38	44.99	4.4
4	46.31	44.73	1.6
6	45.41	44.21	1.2
7	44.03	43.96	—
10	42.39	43.22	—
13	40.60	42.51	—
20	39.50	40.95	—

Notes. Column (1): as measured. Column (2): smoothed value. Column (3): column (1) less (2). Errors became high towards the foot of column (3). The values in column (2) are derived, knowing the decay characteristics of the 'active' solution used, to give the best fit in two respects—(i) to account for all measured 'activity' from about 10 December onwards, so that they represent a smoothed curve for column (1) after that date; and (ii) to make the logarithm of column (3) to plot as a straight line.

Confirmatory Experiments

Two further tests were made with pieces of *F. serratus* (Exps. *T* and *V*), of which the results essentially confirm the foregoing.

(i) Aliquot parts of 50 ml. sea water, activated with 1 ml. of an 'active' solution on 27 October, were placed in tubes *T* and *U*. In tube *T* was then placed a piece of *F. serratus* frond 1.05 g. in weight, and *U* kept as control. Both tubes were sampled 2 days later. The 'decay' curves are given in Fig. 4.

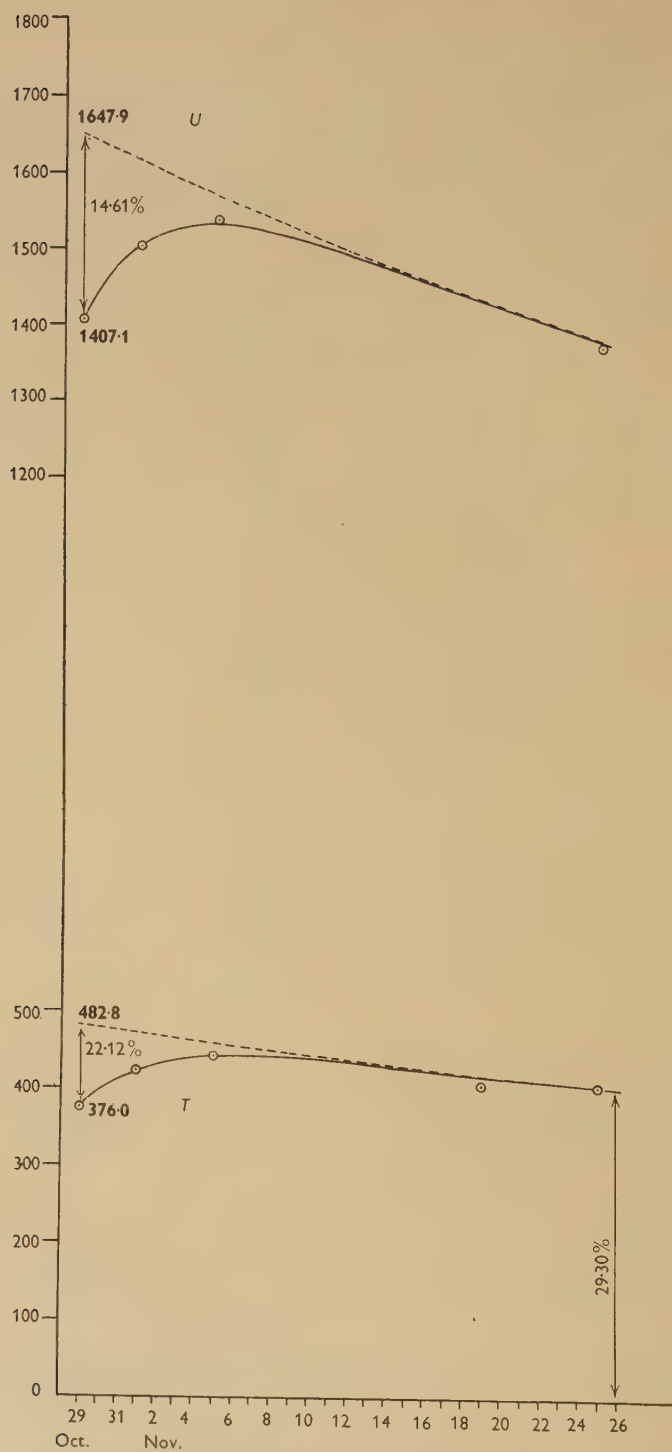


Fig. 4. 'Decay' curves of specimens of 'activated' sea water, as in Fig. 2. *T*, water which had contained a piece of *Fucus serratus* (1.05 g. in 25.5 ml. of sea water). *U*, control. 'Activity' in arbitrary units.

from which a close resemblance to Fig. 2 at once comes to notice. The value of the sample from *T* is at first 26.72% that of *U* and increases to 29.65%. Thus, reasoning as before, 1.05 g. of weed is equivalent to

$$\frac{25.5 \times 0.7035}{0.2965} = 60.5 \text{ ml. of sea water.}$$

This is a weight of 62.14 g. The degree of concentration of the strontium is thus as much as 59 times.

This experiment thus suggests an even higher concentration of strontium in the weed, but the failure, in this particular experiment, to measure the divided volumes exactly may have introduced an error of 3 or possibly 5%. There is partial yttrium deficiency in both *T* and *U*, as was found in Exp. R.

(ii) On 29 October another similar experiment was set up. This time the division of the 'activated' sea water was precise. The 'activity' of the water was less than before. To 50 ml. of 'outside' sea water was added 0.5 ml. of 'active solution *D*' (*D*=the September solution diluted $\times 560$). Into tube *V* was placed 2.9 g. of *F. serratus*, and tube *W* was kept as control. The tubes had been treated with strong cleaning fluid and, probably as a result, hardly any yttrium was taken up by the control. Specimens were taken on 3 November, 5 days later. The 'decay' curves are given in Fig. 5. The final percentage of the 'activity' of the water in *V* compared with *W* is 18.80%. Thus 2.9 g. of weed is equivalent to

$$\frac{25.25 \times 0.812}{0.188} = 109.1 \text{ ml.} = 112.0 \text{ g. of sea water,}$$

or 38.6 times the weight of the weed.

Rhodomenia was again tested on a later occasion (3 December). The 'activated' sea water used was that which had served as control for the previous experiment, i.e. from tube *Q*. Of this 20 ml. were drawn off and placed in tube *L*, the remaining 4 ml., or so, were kept as control. In tube *L* was placed 0.78 g. of *Rhodomenia* frond. The water was sampled on 8 December. The 'activity' curves, shown in Fig. 6, are similar to those in Fig. 1, the alga-treated water showing heavy yttrium deficiency but no strontium deficiency. As the solution is 6 weeks 'staler', there will be rather more yttrium (relatively) present at the start; and, since the ratio $\text{Sr}^{89} : \text{Sr}^{90}$ is now lower by nearly half, the 'decay' of the equilibrium mixture is decidedly slower.

The 'recovery' of the alga-treated water is so complete, as to suggest that the alga had not taken up any 'active' strontium at all. At least it seems that the weed had much less diluting effect than an equivalent weight of water. But again it has taken up almost all available yttrium (probably less had gone on the glass in the clean boiling tube containing the 20 ml. than in the control tube, the original tube *Q*, which had *not* been in cleaning fluid and had been

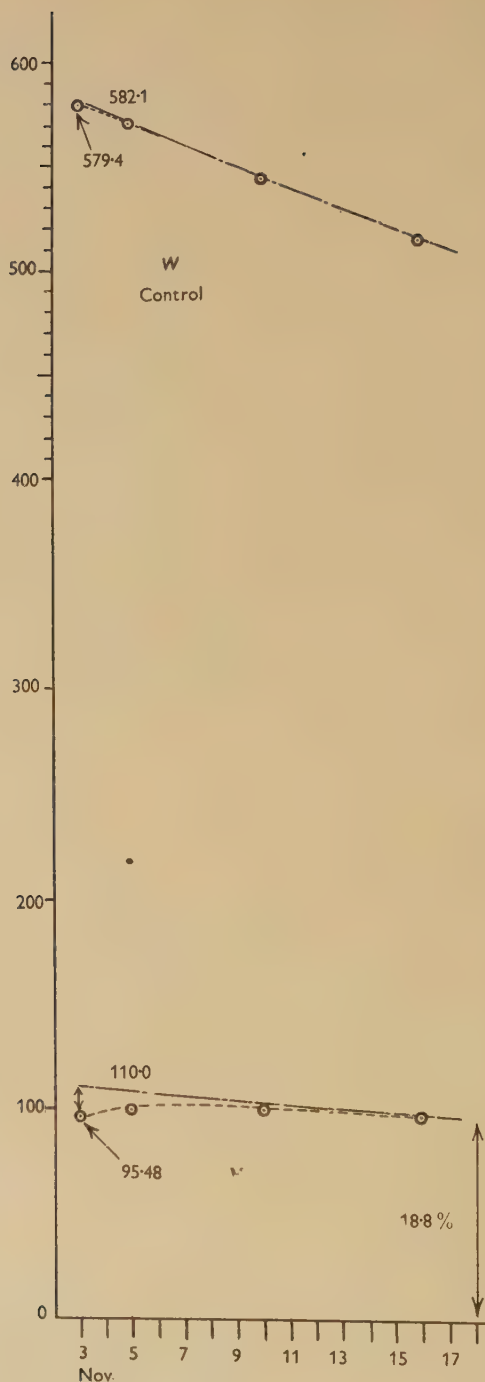


Fig. 5. Similar 'decay' curves as in Figs. 2 and 4. *V*, water which had contained *Fucus serratus* (2.90 g. in 25.25 ml. of sea water). *W*, control.

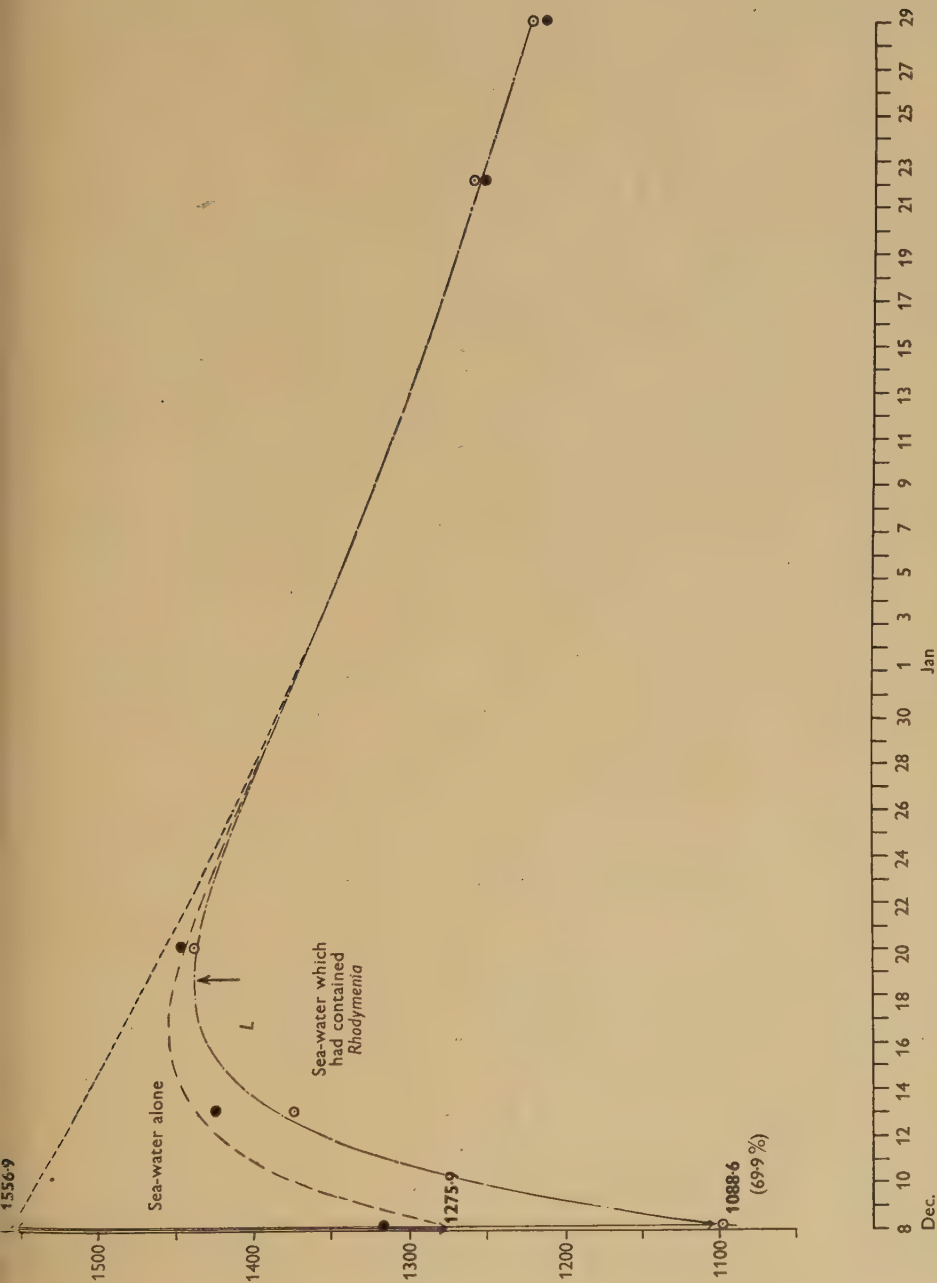


Fig. 6. 'Decay' curve (L) of specimen of activated sea water in which a piece of *Rhodomenia* frond (0.78 g. in 20 ml. of sea water) had been placed, as in experiment shown in Fig. 1. ○—○, specimen of alga-treated water. ●—●, control (in different type of vessel). -----, 'decay' curve of equilibrium mixture. 'Activity' in arbitrary units. Other particulars as before.

standing with sea water for some 6 weeks). Calculation shows that the expected percentage of Y^{90} on 8 December was 30.59%, and the percentage absorbed was

$$100 - \frac{1097.7}{1558.4} \times 100 = 100 - 70.45 = 29.55\%.$$

The closeness of these two figures indicates an absorption of all or 'very nearly all' the Y^{90} .

Again corroboration is provided by examination of the weed itself. A mounted specimen was investigated in some detail, being one that was chosen for a new estimate of the exact half-life of Y^{90} . The damp fragment of frond, well washed and swilled in clean sea water, followed by distilled water, was fixed to a microscope slide by the covering of a broad strip of cellophane adhesive. The piece of weed was thus firmly pressed down by a protective layer which proved very resistant to rough treatment. It has provided a virtually permanent mount. Since we are only concerned with 'decay' characteristics, the loss of 'activity' through absorption by the cellophane covering is immaterial. Duplicate measurements were made in two counter positions. The 'decay' curves are precisely similar to that shown in Fig. 3 (curve *P*), and their ultimate analyses are given in Table II. If 4660 represents the 'activity' of the specimen on 8 December, then only 22, or less than 0.5%, was due to strontium—all the rest represents excess yttrium.¹

In passing, it may be mentioned that the half-life of Y^{90} was estimated as being 63.4 hr. (2.642 days). This value has been adopted in the present computations. It is close to an average of various estimates given to date by different authorities.

An Experiment with other Algae

Before attempting to interpret the results already described it is well to examine the behaviour of some other species of marine algae. How far, it may be asked, does the contrast found between *Fucus serratus* and *Rhodomenia palmata* reflect a constant difference between brown algae and red algae as a whole?

Experiment *J* was set up on 19 and 20 November. A volume of 250 ml. of freshly collected sea water was treated with some of the 'active' solution received in September. From a burette successive fractions of 20 ml. were drawn off into boiling tubes. There were twelve of these altogether, ten designated by the letters *A* to *J*, and two held as a control. All the boiling tubes used had been well cleaned with strong chromate cleaning solution.

The tubes *J_A* to *J_J* contained pieces of different kinds of algae. All tubes were sampled after an interval of 3 days. The main particulars, both of the set-up and of the results, are given in Table III. The 'decay' curves are shown in Fig. 7.

¹ Absorption of some of the β -rays by the thin cellophane covering may have somewhat favoured the Y^{90} at the expense of the Sr.

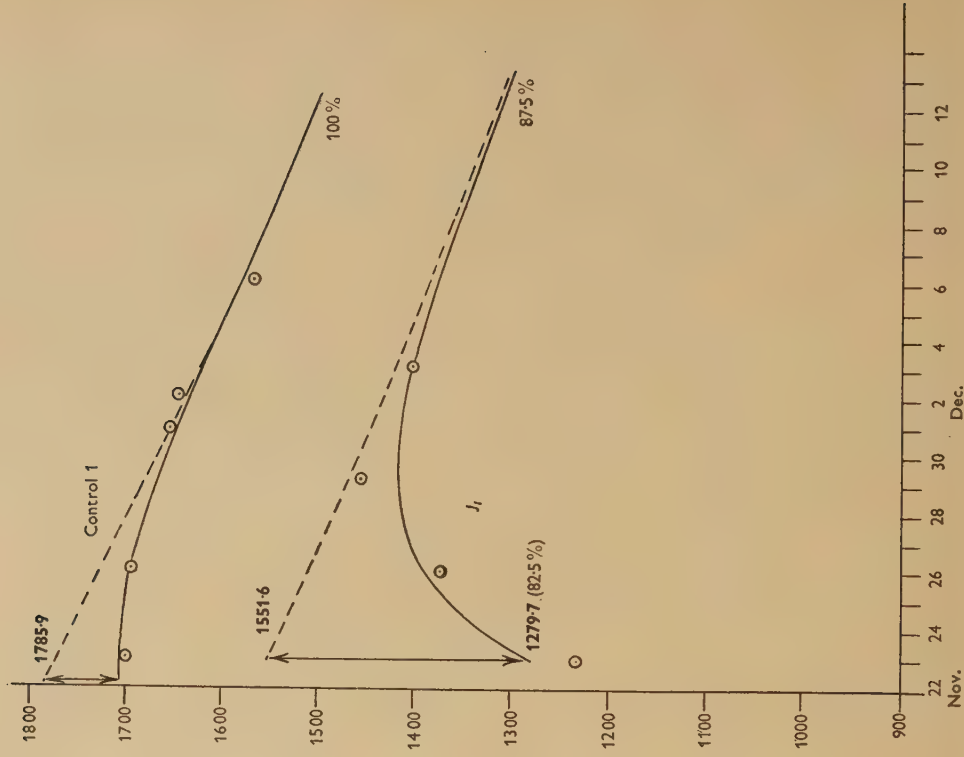
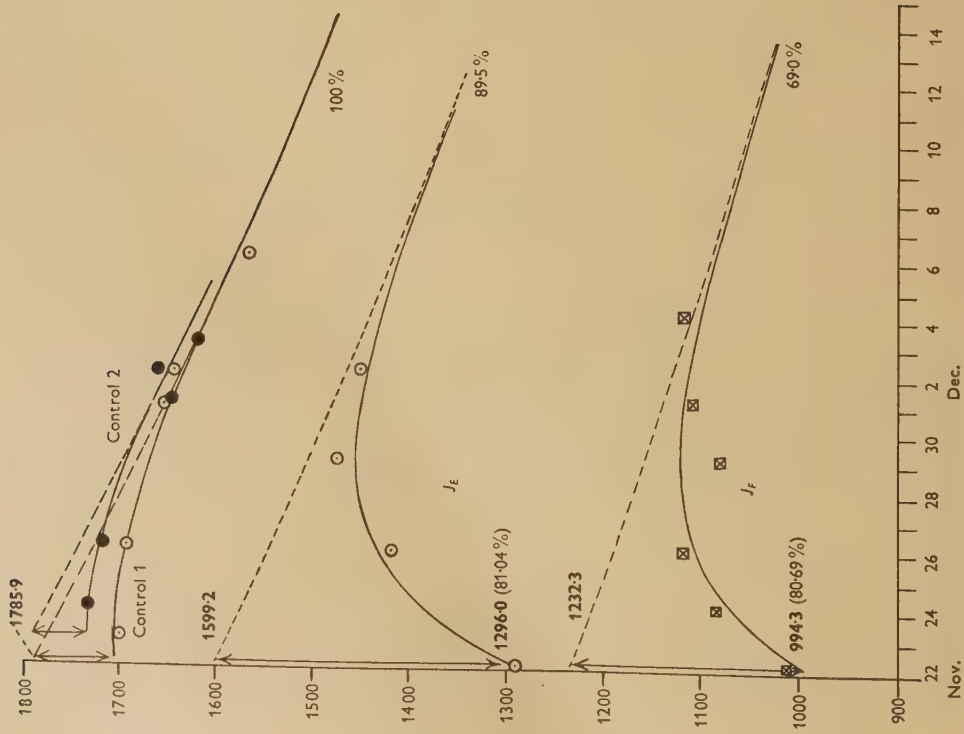
TABLE II. 'DECAY' OF 'ACTIVATED' *RHODYMENIA* FROND (SPECIMEN L)

Two independent analyses at two counter positions. The 'activity' units for position 1 are reduced by a factor of 2.92 to make them very nearly comparable with the measurements for position 2. Further particulars as in Table I.

Position 1 ($\div 2.92$)					Position 2			
Date	Time	(1)	(2)	(3)	Time	(1)	(2)	(3)
		Total activity	Part due to Sr equilibrium mixture	Part due to excess Y^{90}		Total activity	Part due to Sr equilibrium mixture	Part due to excess Y^{90}
8 Dec.	4.54	4659.3	21.9	4637.4	5.29	4682.8	23.2	4659.6
9	5.50	3625.7	21.8	3603.9	6.55	3582.4	23.1	3559.3
10	5.50	2808.4	21.7	2786.7	6.39	2776.5	23.0	2753.5
11	3.48	2162.3	21.5	2140.8	4.46	2179.8	22.9	2156.9
13	12.22	1367.3	21.3	1346.0	3.5	1313.8	22.6	1291.2
14	1.48	1034.8	21.2	1013.6	2.55	1010.6	22.5	988.1
15	12.21	817.5	21.07	796.44	1.32	805.6	22.4	783.2
16	6.41	588.08	20.95	567.13	2.11	622.8	22.2	600.6
17	2.48	478.60	20.84	457.76	5.43	593.9		571.7
18	12.15	383.15	20.73	362.42	1.30	487.35	22.12	465.23
20	1.33	229.30	20.52	208.79	1.26	378.50	22.00	356.50
21	1.47	181.54	20.41	161.13	11.56	234.20	21.78	212.42
22	1.45	142.53	20.31	122.22	12.21	184.48	21.66	162.82
23	1.47	114.62	20.20	94.42	12.36	146.83	21.55	125.28
24	1.39	95.17	20.10	75.07	12.31	117.44	21.45	95.99
26	12.35	64.04	19.90	44.14	12.35	96.46	21.34	75.12
28	2.2	44.97	19.71	25.26	11.46	66.46	21.13	45.33
29	1.59	39.48	19.61	19.87	12.29	45.86	20.92	24.94
30	2.56	34.41	19.52	14.89	12.36	40.68	20.82	19.86
17 Jan.	6.8	16.97	18.00	—	1.13	36.92	20.71	16.21
18	1.44	16.97	17.94	—	—	—	—	—
18	6.38	16.95	17.92	—	12.18	16.89	19.05	—
					5.13	17.45	19.03	—

TABLE III. THE RESULTS OF EXPERIMENT J

Species	Tube no.	Weight of weed (g.)	Initial 'activity'	Final 'activity' in % of control	Degree of strontium concentration	Degree of yttrium absorption
<i>Fucus serratus</i> L.	J _A	1.74	361 (22. xi)	23.03	39.5	Much
<i>F. serratus</i> (in dark)	J _B	1.74	478 (22. xi)	28.23	30.0	Much
<i>F. vesiculosus</i> L.	J _D	3.41	326 (22. xi)	20.46	23.4	Nearly all
<i>F. vesiculosus</i> var. <i>evesiculosus</i> Cotton (young growth)	J _H	3.32	314 (23. xi)	15.13	34.7	Little
<i>Ascophyllum nodosum</i> Le Jol	J _G	5.01	242 (22. xi)	15.98	21.6	All (or nearly all)
<i>Laminaria digitata</i> (L.) Lamour.	J _O	1.55	747 (22. xi)	48.41	14.1	Very much
<i>Laminaria digitata</i> (L.) Lamour.	J _J	6.29	286 (23. xi)	18.55	14.3	Some
<i>Chondrus crispus</i> Stackh.	J _E	1.45	1296 (22. xi)	89.5	1.66	All (or nearly all)
<i>Gigartina stellata</i> Batt.	J _F	4.2	994 (22. xi)	69.0	2.20	All (or nearly all)
<i>Ulva lactuca</i> L.	J _I	2.54	1280 (23. xi)	87.5	1.16	All (or nearly all)
Control 1	—	—	1708 (22. xi)	100.0	—	Little
Control 2	—	—	1745 (23. xi)	—	—	Very little



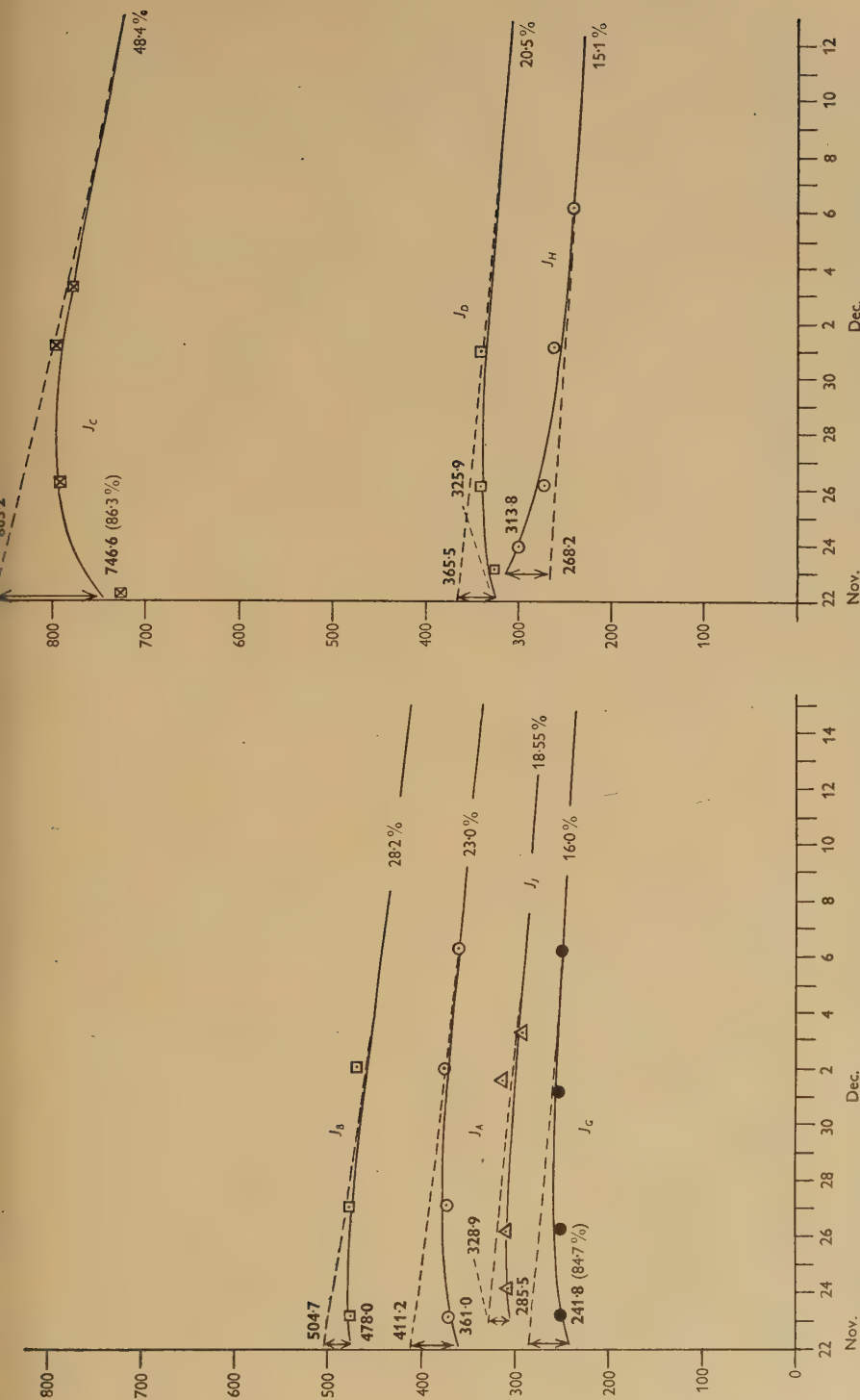


Fig. 7. Results of Exp. $\mathcal{J}$: 'decay' curves of specimens of 'activated' sea water which had contained pieces of various Algae, compared with a control of 'activated' sea water without additions. All tubes contained 20 ml. of sea water, and the weeds were added as follows: $\mathcal{J}_A$, 1.74 g. of *Fucus serratus*; $\mathcal{J}_B$, 1.74 g. of *F. serratus*; $\mathcal{J}_C$, 1.55 g. of *Laminaria digitata*; $\mathcal{J}_D$, 3.41 g. of *Fucus vesiculosus*; $\mathcal{J}_E$, 1.45 g. of *Chondrus crispus*; $\mathcal{J}_F$, 4.2 g. of *Gigartina stellata*; $\mathcal{J}_G$, 5.01 g. of *Ascophyllum nodosum*; $\mathcal{J}_H$, 3.32 g. of *Fucus vesiculosus* var. *vesiculosus*; $\mathcal{J}_I$, 2.54 g. of *Ulva lactuca*; $\mathcal{J}_J$, 6.29 g. of *Laminaria digitata*.

Final readings, critical in determining the relative equilibrium values, were made in March 1949, and are not shown (the curves are thus fitted to more points than are shown in the Figure). Other details as in Figs. 1 and 2.

The two control tubes give nearly identical results which can be combined. They show but small indication of Y^{90} 'recovery', particularly Control 2, indicating that little yttrium can have been taken up by the clean glass of the tubes. This fact shows that yttrium does not necessarily adsorb on *any* available surface, a point of some significance (see p. 622).

The two red algae tested, *Chondrus crispus* Stackh. ($\mathcal{F}_E$) and *Gigartina stellata* Batt. ($\mathcal{F}_F$) behave essentially in the same way as *Rhodymenia*. They show a heavy absorption of yttrium, and no important concentration of strontium. There was, however, a slight differential uptake of strontium which was not observed in *Rhodymenia*. Thus the addition of 1.45 g. of *Chondrus* (to 20 ml. of sea water) was equivalent to diluting with $[20 \times 10.5/89.5 =] 2.35$ ml. of sea water = 2.41 g., or concentration by a factor of 1.66; while the addition of 4.2 g. of *Gigartina* was equivalent to diluting with $[20 \times 31/99 =] 8.99$ ml. of sea water = 9.23 g., or concentration by a factor of 2.20.

The taking up by *Chondrus* of a limited amount of strontium was verified from a mounted specimen of frond. The decay curve indicates that, of an initial 'activity' of 3828, about 3203 was due to yttrium and 625 to strontium.

If 625 represents a concentration of Sr by a factor of 1.66, then a rough estimate of the degree of concentration of the Y might be obtained as follows. On 22 November the percentage due to $Sr^{89} + Sr^{90}$ was 83.20 and to Y^{90} 16.80. The factor by which the yttrium is concentrated could be regarded as

$$\frac{3203 \times 83.2 \times 1.66}{625 \times 16.8} = 42.1.$$

The green alga *Ulva* ($\mathcal{F}_I$) gave a result resembling that previously described for *Rhodymenia*. There was a maximum absorption of yttrium, and scarcely any differential absorption of strontium. Addition of 2.54 g. of the frond was equivalent to diluting with $[20 \times 12.5/87.5 =] 2.86$ ml. of sea water = 2.93 g., or concentrating by a factor of about 1.16.

Confirmation was again obtained from a mount of a piece of the weed. This specimen was measured frequently and used for the purpose of determining the actual decay constant of Y^{90} (Fig. 8, Table IV). Final analysis of the figures indicates that, of the initial 'activity' of 5009 (on 3 December) only some 22.5 was due to strontium (27 to the strontium 'equilibrium' mixture and 4982 to excess yttrium). If it is supposed that the 27 represents simple weight-for-weight dilution of strontium, then the yttrium appears to have been concentrated by a factor of $4982/27 \times 81.7/18.3 = 824$.

Coming to the brown algae, a confirmatory experiment with *Fucus serratus* L. ($\mathcal{F}_A$) may first be mentioned. As before, the water showed a big deficiency of strontium and a certain deficiency of yttrium. The final 'activity' of the specimen measured was some 23.03% of the control. Thus the addition of

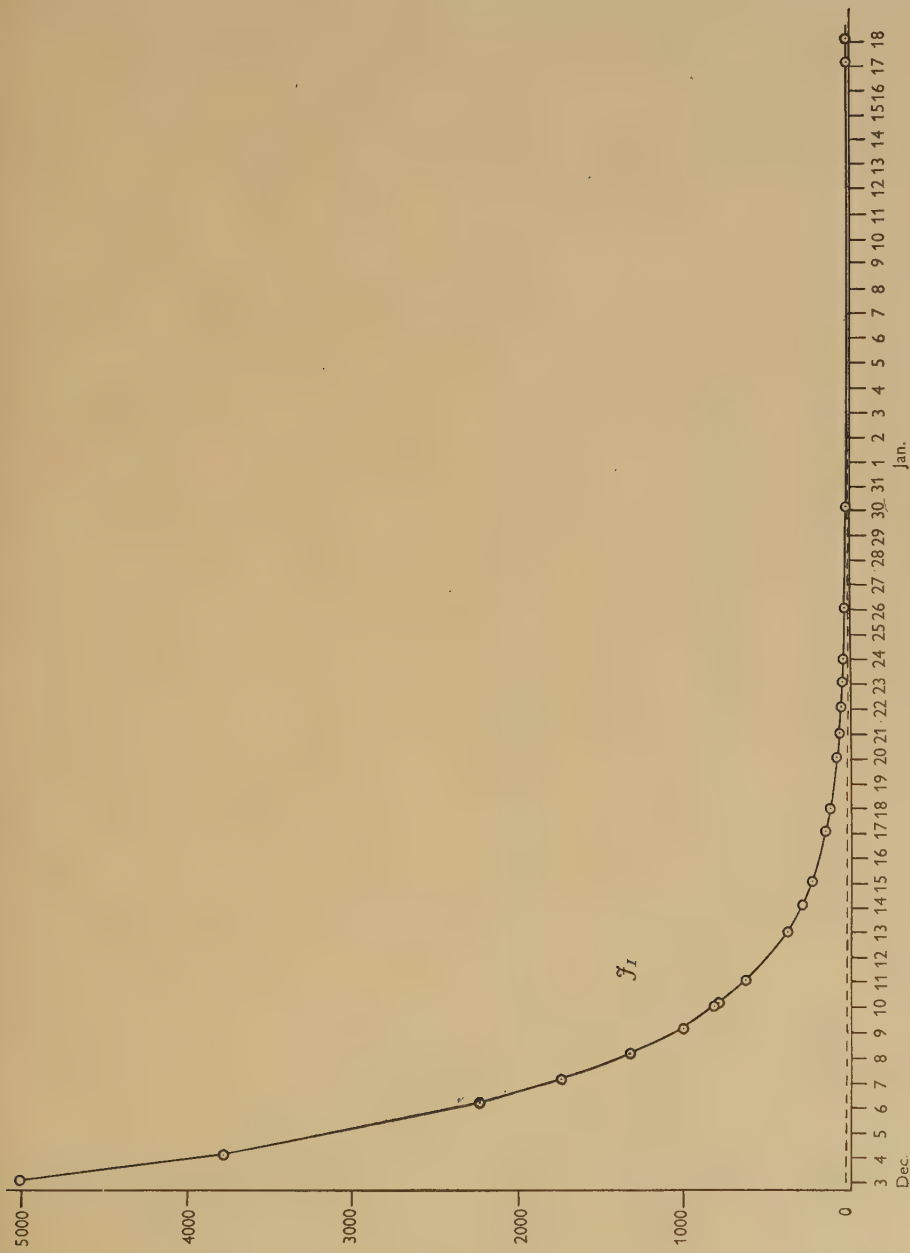


Fig. 8. 'Decay' curve of a mounted piece of *Ulva lactuca* (from tube J_I), as in Fig. 3.

1.74 g. of weed was equivalent to diluting with $20 \times 77.0/23.0 = 66.87$ ml. of sea water, or 68.67 g. The strontium taken up must have been concentrated in the weed by a factor of 39.5. This is the order of result already obtained.

Another sample of *F. serratus* ($\mathcal{F}_B$) was kept in the dark, the tube being well shielded in a box kept under the same table as the other tubes. The sample of weed was made as nearly as possible identical with the other ($\mathcal{F}_A$), and its weight was adjusted so as to be the same (1.74 g.). A specimen of the water

TABLE IV. 'DECAY' OF 'ACTIVATED' *ULVA* FROND (SPECIMEN $\mathcal{F}_I$)

'Activity' (in arbitrary units) of a specimen mounted on 3 December and measured at intervals until equilibrium was reached. Details as in Table I

		(1)	(2)	(3)
	Time	Total	Part due to	Part due to
	(p.m.)	'activity'	Sr equilibrium	excess Y^{90}
			mixture	
3 Dec.	1.32	5009.0	27.0	4982.0
4	2.35	3778.7	26.7	3752.0
6	4.00	2240.5	26.3	2214.2
7	3.45	1746.1	26.1	1720.1
8	4.09	1328.2	25.8	1302.4
9	5.00	1002.8	25.6	977.2
10	2.49	815.9	25.4	790.5
10	5.05	786.3	25.4	760.9
11	2.40	627.1	25.2	601.8
13	1.51	385.81	24.77	361.04
14	4.11	289.46	24.54	264.92
15	2.58	232.45	24.35	208.10
17	3.53	147.62	23.96	123.66
18	2.39	121.39	23.78	97.61
20	3.32	81.47	23.40	58.07
21	3.22	66.19	23.22	42.97
22	3.21	56.43	23.03	33.40
23	3.10	49.19	22.86	26.33
24	2.45	41.93	22.68	19.25
26	2.22	33.79	22.35	11.44
30	4.43	25.72	21.66	4.06
17 Jan.	4.48	20.46	19.05	—
18	3.16	18.26	18.93	—

Note. The earlier counts were run for about 60 mins. and the later from 60 to 90 min.

was taken after 3 days, and again after 10 days. The first specimen showed that the weed had taken up a lot of 'active' strontium as usual, though rather less than in the sample kept in the light. This proved at least that active photosynthesis is not essential for the uptake of the strontium. When the second specimen was taken the weed was clearly dead. Though there was no bacterial scum or cloud, and though the weed had not started to disintegrate, there was a distinct odour of decay and the water had turned bluish green. The second specimen showed that only a fraction of the 'active' Sr had returned to the sea water, the concentration factor having fallen from 30.0 to 22.5. Thus 75% of the amount originally taken up remained in the weed. Exactly the

same fraction also remained in the sample $\mathcal{F}_A$ when this was killed by heating, the concentration factor falling from 39.47 to 29.83.

Two other tubes were given to *F. vesiculosus* L. One sample, of 3.41 g., was of a well-grown typical piece of frond with a number of vesicles ($\mathcal{F}_D$); the other, of 3.32 g., was of young fronds of a non-vesicled form (var. *evesiculosus* Cotton), growing in the upper part of the shore below the Laboratory ($\mathcal{F}_H$).

Both took up a lot of strontium, especially the non-vesicled form. The addition of the 3.32 g. of this weed was equivalent to dilution with

$$20 \times 84.87/15.13 = 112.19 \text{ ml. of sea water} = 115.22 \text{ g.}$$

The factor for the concentration of strontium is thus 34.7. For the typical sample ($\mathcal{F}_D$) the concentration factor is 23.4.

An unexpected difference between these two samples is seen in their relation to yttrium. The typical sample ($\mathcal{F}_D$) appears to have taken up all, or nearly all, the available yttrium, a very marked recovery being shown by the specimen of the water. Not so, however, with the var. *evesiculosus* sample ($\mathcal{F}_H$). The specimen of the water surrounding it was not deficient in yttrium in any way: within the limits of accuracy of the 'decay' curve it was either in equilibrium at the start, or, more probably, had a small excess of yttrium, as distinctly shown in Fig. 7 ($\mathcal{F}_H$). The last alternative is proved to be correct, as two specimens of the actual weed from tube $\mathcal{F}_H$ were mounted and their 'decay' characteristics observed. The 'decay' curve of both these specimens shows evident yttrium recovery at the start (the inverse, of course, to the behaviour of the water). The extent of recovery indicates that the degree of yttrium concentration in the weed, if indeed appreciable, was far less than that of strontium. Among the algae tested *F. vesiculosus* var. *evesiculosus* was the only one to behave in this way.

Ascophyllum nodosum Le Jol absorbs much strontium, concentrating it to the extent of some 21 times, and apparently much yttrium.

There remain the two samples of *Laminaria digitata* (L.) Lamour. One ($\mathcal{F}_C$) consisted of a piece of frond, 1.55 g. in weight; the other ($\mathcal{F}_J$) of a large piece of the base of the frond with some stipe of which a length, which became desiccated, protruded from the water. The submerged part of the last weighed 6.29 g.

The results of these two samples essentially agree. Much Y^{90} appears to have been taken up by the *Laminaria*, best demonstrated by the 'recovery' in the $\mathcal{F}_C$ curve. At the same time a fair amount of 'active' Sr was also taken up, the concentration factor for $\mathcal{F}_C$ being 14.1 and for $\mathcal{F}_J$ 14.3. The two values derived from such different weights of weed are in excellent agreement.

Thus all the four brown algae tested agreed in the general property of concentrating 'active' strontium, the effectiveness in this respect being shown in the following sequence: *Fucus serratus*, *F. vesiculosus*, *Ascophyllum nodosum*, and *Laminaria digitata*.

INTERPRETATION IN TERMS OF IONIC EXCHANGE

How is this capacity for absorbing the 'active' strontium or yttrium to be interpreted or visualized? At the risk of over-simplification three main possibilities have to be considered: (i) adsorption, (ii) ionic exchange, (iii) extraction.

The capacity for metallic ions to become adsorbed on surfaces is well known. In sea water, elements present in very small concentrations may readily do this, as, for example, Harvey (1937, 1949) finds with iron and manganese. Mud particles, faecal pellets, and parts of organisms of all sizes, may at times provide suitable surfaces. The extent to which any element will get adsorbed will depend on the degree of previous saturation of the surface with the element. This process, it may be noted, involves active removal of the element as a whole from solution, including any radioactive isotopes which may have been added to it; and might easily go to the extent of removing all except an insignificant trace. The marine chemist has acquired the habit when dealing with an element of low concentration, of enquiring how much of it may be getting adsorbed on the apparatus with which the water is brought in contact.

The phenomenon of ionic exchange is quite different. The concentration of a given element inside an organism may not be the same as that in the water outside. For example, a much higher concentration may be maintained by the organism, which does work against osmotic forces. But, whatever the relative concentration in the organism, there may be free exchange between the ions of the outside water and those of the internal fluids. If some of the ions in the water outside are labelled in some way, after an interval these will be found distributed inside the organism as well as outside. This will happen when a radioactive isotope is introduced. At first all its ions will be outside; but after an interval these will become generally distributed at random throughout the population of the particular ion. So they will be most numerous where that element is concentrated, and vice versa. If the element is concentrated in the organism, say an alga, then the radioactive ions will be found to enter the alga, and the extent to which they aggregate in the weed will provide an exact measure of the relative concentration of the element in the weed. There is, therefore, no passage of the element as a whole into the weed, and the respective concentrations in weed and water remain unaltered (assuming the amount of active isotope is negligible). There is simply a random interchange of ions amongst the existing population. Ion exchange is only liable to reduce the amount of 'active' isotope in the external medium to a negligible quantity if there is very great difference between the concentration inside and outside the weed, and this will not frequently occur. Increasing the weight of the weed added to a given volume of water becomes increasingly ineffective: the effect is in no way additive.

The third possibility has features in common with both the preceding. Extraction resembles adsorption in that it involves removal by the organism of the element as a whole, but differs in that the ions pass into the organism where they may be 'locked up'—as, for example, calcium in skeletal tissue or mollusc shells. At the same time extraction may develop as a special case of ionic exchange when ions are progressively removed from circulation inside the organism so that fewer return to the outside solution than are taken from it. As in simple ionic exchange, passage of 'active' ions into, for example, an alga indicates that the weed has a higher concentration of the element inside it, but where extraction is going on there is active uptake of the element as a whole, which may proceed steadily until all the element is removed from solution. The attainment of an equilibrium is less probable, and, within limits, the effect of increasing the amount of weed is likely to be additive.

With strontium which exists in comparative plenty in sea water (about 0.04% of total salts, = 14 g./m.³), it is assumed that the chance of uptake by adsorption is negligible. First, all surfaces will already be saturated with the quite small quantities which may be taken up in this way. Secondly, the proportion of strontium which may be found adsorbed at any one moment is likely to be small, or very small, compared with that of ions free in solution; because of which the loss of radioactive ions by ionic exchange with surfaces already saturated may be supposed to be negligible.

As far as the red and brown algae considered here are concerned, it seems almost certain that progressive extraction can be ruled out. The consideration is likely to arise only with calcareous algae, amongst which there might be possibilities of precipitation of strontium along with the calcium carbonate. In the results obtained above it seems that the main effects occurred quickly, and the loss of 'activity' certainly did not vary directly with the weight of the weed.

Straightforward ionic exchange seems the only possible interpretation, which is positively indicated by the sort of effects obtained when the weight of the weed is increased. The two samples of *L. digitata* ($\mathcal{F}_C$ and $\mathcal{F}_J$) are striking in this respect from two very dissimilar weights, 1.55 and 6.29 g., and identical estimate of the degree of concentration of the strontium is obtained. As a plausible working hypothesis, therefore, the uptake of strontium is regarded as essentially a matter of ionic exchange. If, as happens, the radioactive Sr ions disappear from the water into the weed it is because the weed all along contains a heavier concentration of strontium than the water. Moreover, the measure of the degree of concentration of the 'active' Sr ions in the weed (as given in Table III on a weight for weight basis) is a measure of the concentration of the weed's normal strontium content. It is concluded, therefore, that *Fucus serratus* has about 40 times as much strontium as sea water¹, *Laminaria digitata* about 14 times, while no or very little concentration or even positive exclusion is shown by three red algae and *Ulva lactuca*.

¹ There is now direct support for this conclusion: see p. 625.

The matter is rather different for yttrium. This element has been observed in sea water (see the chapter on the minor constituents of sea water in Harvey, 1945, pp. 31-42), and it appears to be one of many whose concentration is of the order of 1 mg./m.³. It is likely, therefore, that adsorbant surfaces are far from saturated with it. Experience has shown that it quite readily adsorbs on unclean glass, from which it can only be finally removed by strong acid. Uptake by adsorption may therefore play a prominent part in the exchanges of this element, and special technique may be necessary to distinguish between adsorption and ionic exchange. This problem is further discussed below.

EXPERIMENTS WITH CULTURES OF UNICELLULAR ALGAE

Certain preliminary experiments with algal cultures have not yet been developed on an adequate quantitative basis, but some qualitative results may be placed on record at this stage.

A portion of a culture was treated with some 'active' solution. It was allowed to stand until the organisms in the culture had aggregated at the bottom, or near surface, of the liquid. A drop containing the thickest aggregate obtainable of the organism was then withdrawn and compared with another drop from the main volume of the liquid, or from its clearest part. By this means it was hoped to detect differential absorption by the organisms in question, although dense aggregations were usually difficult to obtain and impossible to measure accurately in terms of weight or volume. As before, sample drops consisted of 0.05 c.c.

Chlorella (Exp. M). About 25 c.c. of a culture of *Chlorella*, reproducing at a slow rate, was treated to the extent of giving it an 'activity' of about 950 per 0.05 c.c. (measured from the first stage of the M.R.C. Castle). After standing for a day or two the *Chlorella* cells had tended to aggregate in a green ring at the bottom of the flask. A number of specimen drops were taken from this flask. All showed appreciable yttrium recovery, indicating that the glass wall of the vessel had adsorbed some, but by no means all, of the yttrium. The greatest deficiency of yttrium was each time shown by those drops taken close to the bottom (i.e. against the glass) away from the alga deposit. Drops taken from the bottom to include some of the *Chlorella* aggregate, which was dense enough to give a distinct greenish opacity to the evaporated drops, consistently showed a 5-10% higher 'activity' than other drops. It would seem that the *Chlorella* definitely concentrated some of the strontium, but since the weight of alga involved was not ascertained, no estimate of the degree of concentration can be given.

Chlamydomonas. A series of tubes containing a *Chlamydomonas* culture was used to test lethal doses. From one of the relatively more weakly activated tubes, in which a flourishing colony of the alga had grown and aggregated at the surface, two strongly contrasting drops were obtained—one densely green,

and the other clear to the naked eye (Exp. *Ch*). Rather heavy yttrium recovery took place in both drops, but more in the control than in the drop containing the *Chlamydomonas*. This indicates that some of the yttrium lost from solution had been taken up by the *Chlamydomonas*. There was an appreciably higher 'activity' remaining in the drop containing the alga, some 6% greater than the 'activity' of the clear drop, indicating that the *Chlamydomonas* had also concentrated strontium to some extent.

Nitzschia. On 10 November a fairly dense culture of this diatom was 'activated' with 'active solution A' (The September solution diluted $\times 14$). This was done in the following way. 50 c.c. of fresh sea water was 'activated' with 0.5 c.c. of solution A. This was exactly halved, one half being set aside as control (flask Y). To the other half, 25.25 c.c., were added 10 c.c. of *Nitzschia* culture and a further 0.1 c.c. of solution A. This mixture, comprising 35.35 c.c. (labelled flask X), was stood near a fluorescent source of light.

In the course of hours the diatoms formed a layer on the bottom of the flask, and the main volume of the medium grew steadily clearer. Samples were first taken on 13 November and again on 18 November. The results of the two samples are similar, and very striking (Figs. 9-10).

The curves in Figs. 9-10 show measurements of three drops from the control flask—Y₁, 10 November; Y₂, 13 November; Y₃, 18 November. They show also measurements of two drops taken from the top of the liquid in the diatom flask, and containing very few, if any, diatoms—X₂, 13 November; X₃, 18 November. These drops all behave much alike: their 'activity', within experimental limits, became identical; though at the start there were definitely more signs of yttrium recovery in the X specimens.

In contrast to these, there were three drops taken from the bottom of the flask in an attempt to pick up as much *Nitzschia* deposit as possible—X₁, 13 November; X₄ and X₅, 18 November. In these the liquid looked very brown, though the actual proportional volume of diatom cannot have been great—perhaps, at a guess, one-fiftieth of the 0.05 c.c. drop.

The 'activity' of these drops was great at first—over twice that of the controls, or drops from the top of the same flask.

But 'decay' proceeded fairly rapidly, until in 3 weeks it had virtually fallen to that of the other specimens. It is plainly seen that all the excess 'activity' at the start had been due to excess Y⁹⁰ in the *Nitzschia*-containing drops. (The converse, deficiency of Y⁹⁰, is quite distinct in the clear X drops, as indicated above.)

Nitzschia cells, therefore, are capable of taking up yttrium very heavily.

It may be supposed that this phenomenon is due to the adsorption of yttrium on the diatom. These minute attenuated cells with porous or pitted surfaces present an enormous surface area.

Experimental evidence for this view is provided by the test of killing the

culture. On 23 November the whole flask was heated to nearly boiling point and the cells completely killed. Similar specimens as before were taken on 25 November after settling had taken place. But the results were exactly as before— X_6 , from the top of the flask, gave similar measurements to X_2 and X_3 , and X_7 , with bottom deposit, gave as high a reading as before (X_1 , X_4 , X_5). No yttrium had come out of the dead cells: it is certain that at least

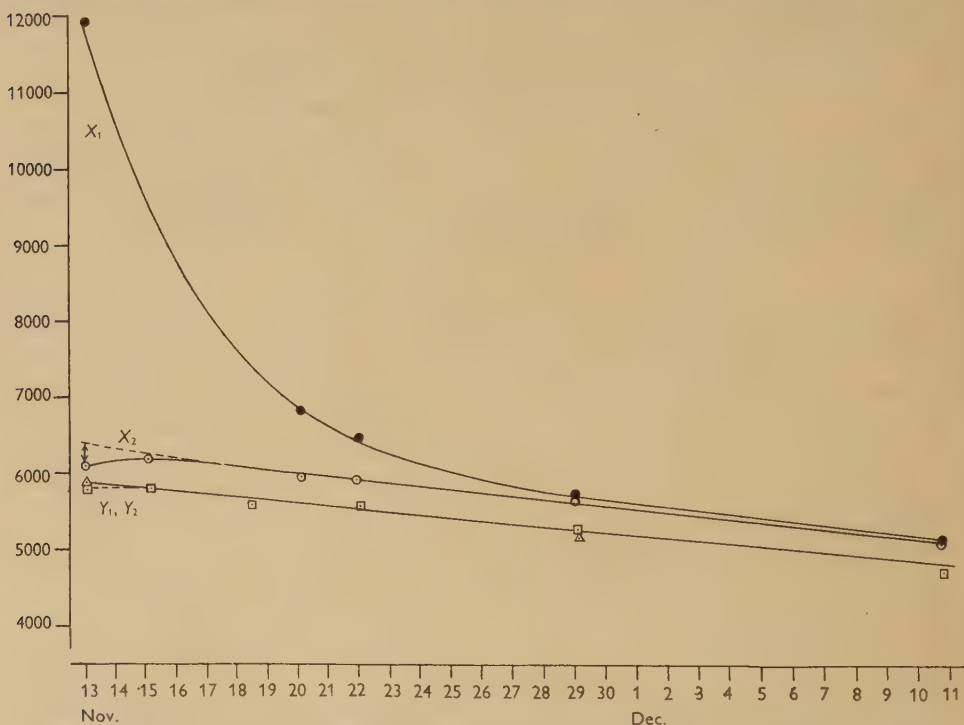


Fig. 9. 'Decay' curve of a specimen of water rich in *Nitzschia* (X_1), compared with culture water more or less free from *Nitzschia* (X_2) and with a sea-water control (Y_2).

a substantial part would have returned to solution (not necessarily all—cf. *Fucus* killed in the same way) had the yttrium been held by simple ionic exchange.

This result suggests that diatoms as a whole, as well as other organisms such as sponges, are potential takers up of yttrium and other metals related to the rare earths. This possibility certainly needs pursuing further.

DISCUSSION

The experiments described above have been essentially exploratory, and any conclusions suggested by them must, in the main, be provisional, awaiting confirmation from the many further lines of experimentation which suggest themselves.

It is, however, clear enough that at least some of the commoner brown algae have a considerable capacity for taking up 'active' strontium ions from the water around them. The provisional explanation is that the weeds have, in their normal make-up, a relatively high content of strontium, and that the 'active' strontium ions enter the alga by simple ionic exchange. It is thus

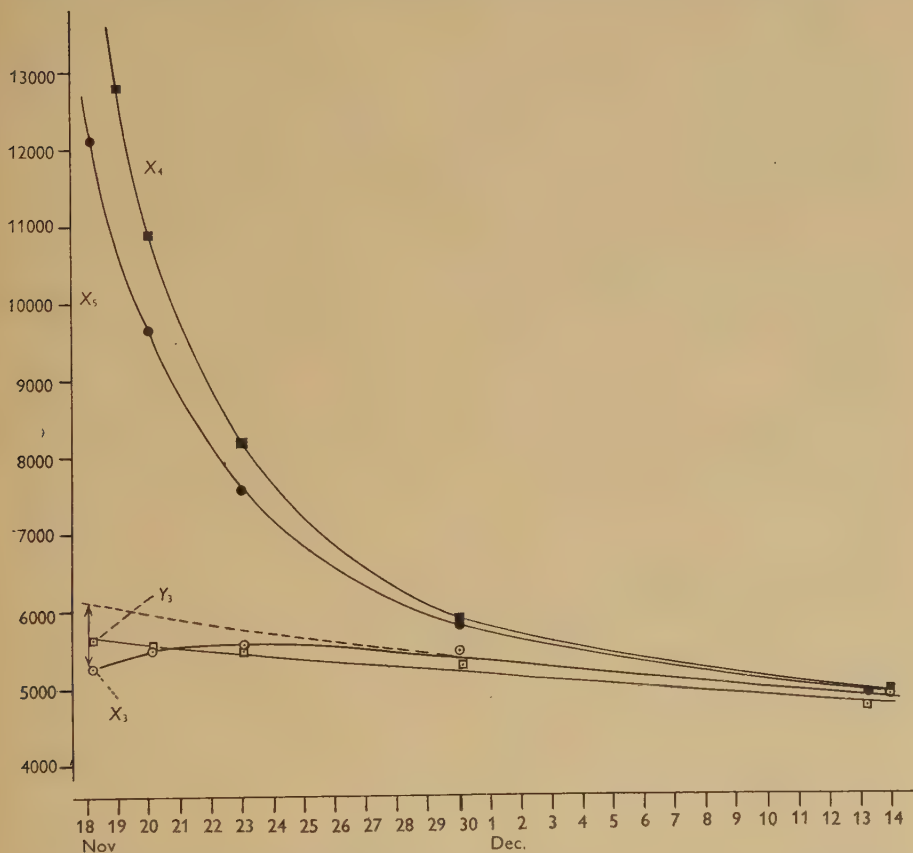


Fig. 10. Repetition of results with *Nitzschia* shown in Fig. 9. X_4 and X_5 are specimens of culture water from the bottom of the flask, rich in *Nitzschia* (cf. X_1). X_3 is a specimen of the clear culture water from the top of the flask (cf. X_2). Y_3 is a second specimen from the control flask.

supposed that there is no actual change in concentration of *total strontium* either in the weed or in the water. This is a straightforward chemical proposition, susceptible of test by direct chemical analysis. If it were not for the unusual difficulties in estimating strontium, owing to its very close affinity to calcium (see Webb, 1938), adequate information on strontium-content of different algae might have been available long ago. As it is, the scanty available

data are suggestive. From Webb's (1937) spectrographically derived data, *Fucus serratus* receptacles and *Sacchorhiza bulbosa* stipe are seen to have had a high Sr/Ca content of about 1/10, three times as great as in sea water. These were the only two out of 23 analysed tissues of marine organisms (mostly animal) in which the Sr/Ca ratio was appreciably greater than that of sea water. By contrast, the ratio in *Ulva lactuca* frond is found to have been about 1/150. Webb's analyses (presented as percentages of total cations in the ash) perhaps suggest that Sr was concentrated to some extent in the two brown-weed samples, but scarcely more than some 4 to 6 times; while in *Ulva* the Sr seems to have been definitely deficient by a factor of at least $\frac{1}{2}$. The only other known published strontium analysis of a marine alga is that by Wilson & Fieldes (1941) for *Macrocystis*, in which significantly enough, the figure given works out at some 14 or 15 times that of sea water,¹ a value which agrees with the concentration here reported for *Laminaria digitata* (Table III, p. 609).

If this provisional explanation is verified², clearly the tracer technique can be introduced to replace the laborious chemical analysis otherwise involved with an element like strontium. The strontium content of dozens of samples of algal species, or of phases or parts of a single species, could be quite rapidly ascertained with a considerable degree of accuracy. This point need not be laboured: the revolution in biochemical technique has already set in.

As already discussed, with a relatively plentiful element like strontium, uptake by adsorption on surfaces may probably be disregarded. With numerous elements, however, of which yttrium is one, which are present in the sea in a concentration of the order of 1 mg./m.³, it may be otherwise.

Yttrium will be subject to ionic exchange as much as strontium. With scarce elements of this type there are likely to be considerable fluctuations in concentration, relatively expressed, of purely local nature. Quite heavy uptake of radioactive ions by, say, weed might be observed, simply because the water in which it had previously been kept had even less of the element than usual. In short, there will be more casual variations in concentration, and less consistent experimental results.

However, effects due to ionic exchange may be overshadowed by those due to adsorption on surfaces, a process which involves actual removal of the element from the water. The tendency for glass surfaces, particularly if not well cleaned, to adsorb yttrium is easily demonstrated. It is likely that the observed affinity of *Nitzschia* for yttrium (p. 619) is the result of adsorption on the surface of this diatom. Perhaps, too, the marked concentration of yttrium by the three red algae and *Ulva* might be purely a matter of adsorption on a surface: the almost complete removal of 'active' yttrium from solution by these weeds, which would otherwise imply an enormous concentration in the

¹ Wilson & Fieldes give values for parts per million of air-dried weed. It is assumed that air-dried weed is one-fifth the wet weight, and wet weight is compared directly with sea water.

² See Postcript, p. 624.

weed compared with the sea water, suggest this explanation. But other considerations must be taken into account before a decision is made.

First, yttrium is not automatically adsorbed on to all surfaces. If glass is well cleaned with strong cleaning solution, there is very little yttrium uptake (Fig. 2(s), Fig. 5(w)). Secondly, the brown algae did not take it up anything like to the same degree as the red algae, and that, indeed, *Fucus vesiculosus* var. *evesciculosus* took up very little. Though it is always possible that the yttrium loss on the glass of the vessel is variable and difficult to allow for exactly, the uptake by brown algae also seems variable and not readily predictable. It is possible therefore that uptake of Y^{90} in the brown algae is chiefly a matter of ionic exchange, while in the red algae and *Ulva* surface adsorption is predominant, and in *Nitzschia* adsorption virtually the sole cause. Further experiments are necessary to clear this matter up.

Of all elements, yttrium is one which has a minimum of biological significance. It plays no special part, as far as is known, or can be visualized, in the chemical exchanges of animals and plants. What purpose, therefore, is served in putting the observations on this element on record? In answer the following points may be brought to notice.

(i) However unimportant yttrium itself may be, its properties and behaviour are probably typical of a number of elements which occur very sparingly in the sea, and of which some are of proved biological importance. Facts derived from yttrium may prove equally applicable to iron, manganese, cobalt, etc., particularly with regard to adsorption phenomena.

(ii) Opportunity has been taken, while yttrium happened to be available for study, of developing technique which can be readily adapted to other elements. Not the least interesting point is that a good deal of information, partly quantitative, can be secured from an element which is (a) present in minute quantities, and (b) not deliberately chemically separated. Yttrium is not easily obtained in pure chemical form, free from the related 'rare earth' elements, etc.; yet, when Y^{90} occurs as a daughter product of Sr^{90} , it is pure and free from contamination of other elements which have similar chemical properties. (Its parent and daughter products are both in different columns of the periodic table.) The technique of using *daughter isotopes* as tracers opens up interesting possibilities.

(iii) It may be a matter of interest when a biological experiment proves capable, unexpectedly, of making a contribution to pure chemistry or physics. The discovery that some red algae and *Ulva* were able to concentrate Y^{90} at the expense of its parent, Sr^{90} , enabled specimens to be prepared from which it is possible to make an apparently accurate estimate of the half-life of Y^{90} . The attempt made by the present writer could no doubt easily be improved on by the same technique, yet it appears to be as reliable as any made hitherto, judging by the small margin of error which the figures obtained seem to allow.

Postscript

Since the above was written the result has become known of an estimate of the strontium content of a sample of *Fucus serratus* ash, determined by the Analytical Group Chemistry Division of A.E.R.E. The ash was prepared at Plymouth by Mr F. A. J. Armstrong from a known weight of weed, and the Sr determination at A.E.R.E. made, after various difficulties had been overcome, by the technique of flame spectrometry.

The strontium content was reported as 0.9 % of the ash, the ash originally representing 5.26 % of the wet weed. The weed therefore contained 0.04734 % of Sr, as compared with the 0.00135 to 0.00140 % believed to be characteristic of sea water. This difference represents a concentration of Sr in the weed by a factor of 34 or 35, and is in excellent agreement with the values derived above for *Fucus serratus*, supporting both the assumption that Sr is concentrated in this and other brown algae, and the validity of employing the tracer technique to provide quantitative assessments of the degree of this concentration.

SUMMARY

Certain marine algae were treated with sea water containing carrier-free radioactive strontium (mixture of Sr^{89} and Sr^{90}), to test whether these ions were taken up by the weeds.

At the same time the behaviour of radioactive yttrium (Y^{90}), which occurred as a short-lived daughter-product of Sr^{90} , was investigated by the expedient of studying the 'decay' characteristics of specimens of water and weed. Promising possibilities of this technique, by which an isotope is made available for study by applying its parent substance, are pointed out.

Radioactive strontium is extracted from sea water by the brown sea-weeds, in particular by *Fucus serratus*.

It is held that this effect is simply a result of ionic exchange, and that the algae regularly contain many times as much strontium in their cell fluids as exists in sea water.

On the ionic exchange hypothesis, it appears that *Fucus serratus* has about 40 times as much strontium as sea water, *F. vesiculosus* about 30, *Ascophyllum nodosum* about 20, and *Laminaria digitata* about 14.

By contrast, red algae and green algae such as *Ulva* extract 'active' strontium only to a small or negligible extent. On the above hypothesis, in *Gigartina* the strontium is concentrated by a factor of about 2, while in *Rhodymenia* it may be less than in the sea.

Radioactive yttrium is heavily taken up by the red algae (*Rhodymenia*, *Gigartina*, *Chondrus*) and by the green alga *Ulva*, even to the extent of depleting the water of this element, or very nearly so.

The yttrium, however, is not usually heavily taken up by the brown algae,

and may (as with a sample of *Fucus vesiculosus* var. *evesiculosus*) be taken up only to quite a small degree.

The diatom *Nitzschia* takes up 'active' yttrium very heavily.

The extraction of yttrium appears to be a matter partly of ionic exchange and partly of *adsorption* on surfaces. It is suggested that both processes may be important with red algae, the former primarily with brown algae, and the latter primarily with *Nitzschia*.

From the 'decay' characteristics of mounted pieces of frond of the red algae and *Ulva*, estimates of the true half-life of Y^{90} were made. The value derived is 63.4 hours (or 2.642 days).

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THE DISTRIBUTION OF LUGWORMS (*ARENICOLA MARINA* L.) OVER THE FLATS AT WHITSTABLE

By Garth Chapman, M.A., Ph.D. and G. E. Newell, B.Sc., Ph.D.

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(Plate I and Text-figs. 1-2)

INTRODUCTION

It has been noted at Whitstable that lugworms (*Arenicola marina* L.) on the Flats are not uniformly scattered (Newell & Chapman, 1948). This is clearly seen in the distribution of castings which tend to be more numerous along straight lines of up to 60 yd. in length. That this effect is not a subjective one is clearly shown by photographs (Pl. I, figs. 1 and 2), by the visibility of the lines to unprejudiced observers as well as by counts of castings in and around the lines, whilst the permanence of the lines (see. p. 630) indicates that they are not due to chance. It also appears that the 'line distribution' is a purely local phenomenon since it occurs only over a restricted area of the Whitstable Flats and has not, apparently, been noticed elsewhere in similar situations. This view has received some confirmation from the late Mr R. Elmhirst and Mr E. M. Venables (private communications).

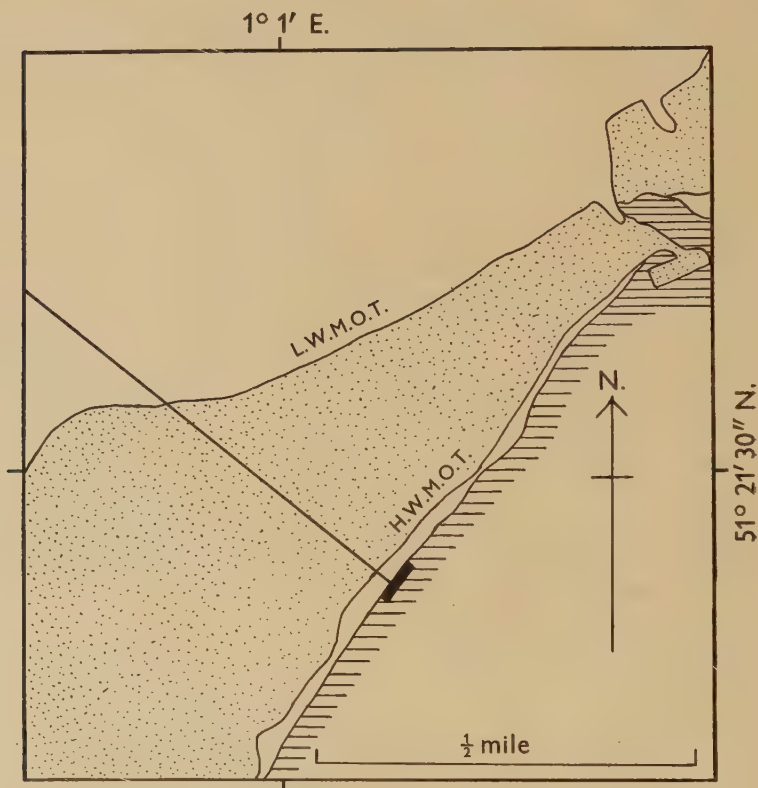
Since a study of the factors affecting the distribution of the lugworms might be of general interest, an attempt was made to find some explanation of the grouping displayed by the castings. These, in a given area, are not necessarily the same in number as the worms, but since throughout this paper figures of the numbers of castings have been used for purposes of comparison and the observations on which the comparisons were made have been done at the same time, it is fair to use the population of castings as an indication of the population of worms.

Experiments carried out on the burrowing of the lugworm (Chapman, 1949) tended to show that the 'hardness' of the marine soil might affect the distribution of these animals, since they seemed to be completely unable to burrow into soil which was made more resistant by the withdrawal of water from it.

It seemed important, therefore, to determine first of all if there were any significant differences in hardness of the soil in different areas of the Flats which might cause patchy distribution. The hardness at different stations was therefore tested by means of the penetrometer used on previous occasions.

VARIATION IN NUMBERS OF WORMS FROM HIGH TO LOW WATER

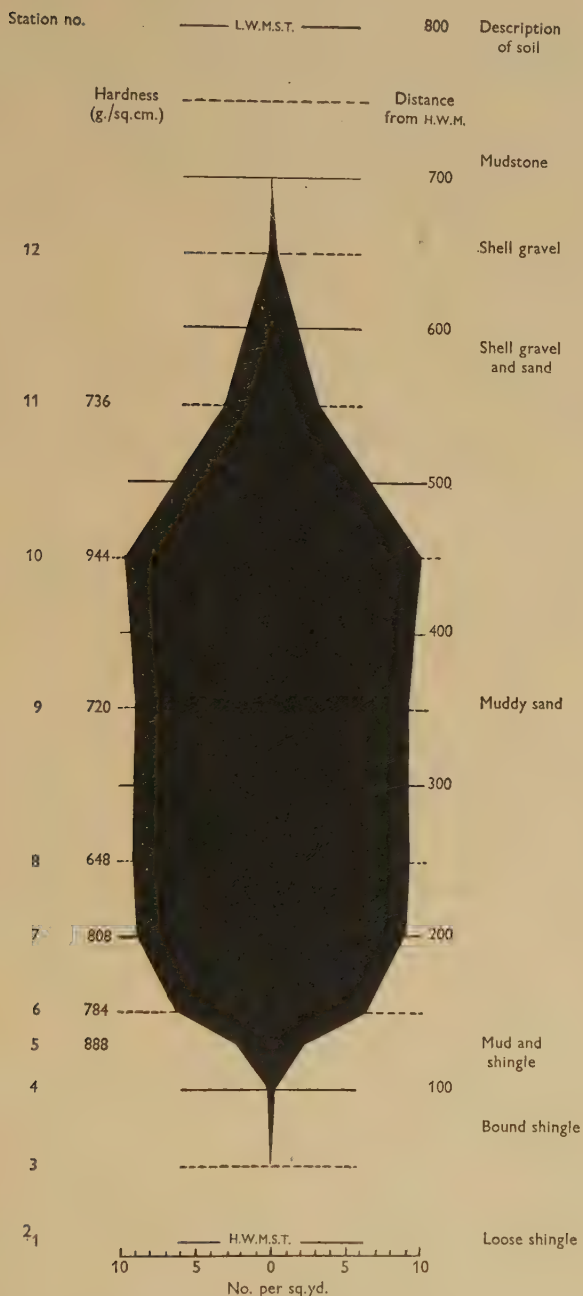
The number of worms per square yard was counted at selected intervals on a transect of the Flats shown in Text-fig. 1. At each station areas of 1 sq.yd. were dug over and examined for lugworms after they had been well broken by the fork. Although the method may be described as 'rough and ready' it is



Text-fig. 1. Transect of intertidal zone at Whitstable along which the lugworm population was determined.

quite adequate for the task involved and capable of yielding consistent results as Newell (1948) has shown. The hardness of the soil in the proximity of the sample was tested with the penetrometer. The results are set out pictorially in Text-fig. 2 in which the hardness of the sand, the mean population of lugworms, and the position on the shore of each station is shown.

It can be seen from Text-fig. 2 that the lugworms are most numerous in the region of the Flats that can be described as muddy sand and that they fall off rapidly in numbers in the shingle bank towards high water and towards the



Text-fig. 2. Diagram showing the numbers of lugworms per sq.yd. in intertidal zone at Whitstable. The hardness, in g./sq.cm., is the mean of twenty readings at each station. The numbers of worms per sq.yd. is a mean of not less than three samples. H.W.M.S.T., high-water mark spring tides; L.W.M.S.T., low-water mark spring tides.

clay that is uncovered at low-water spring tides. In between these two less thickly populated zones there is a region in which no great variation in hardness occurs, at least as shown by penetrometer measurements, but in which the population varies from 1 sq.yd. to another. There may be areas of many square yards in which there is a uniform density of population, which can be described as the 'general population' of the Flats, but this is split up by areas in which the number of worms is greater or less than the 'general population'. (In this survey of the population it is the 'general population' to which the figures of worms per square yard refer.)

The limitation of the population towards high-water mark would appear to be brought about by the increasing scarcity of any soil of sufficiently small particle size in which burrows could be made and also, probably, by the drying of the soil during low water. The limitation of the population towards low-tide mark appears to be brought about by the decrease in depth of the sand and fine gravel which overlies the clay. Other evidence in favour of this hypothesis will be given below.

In short, it would appear that there is insufficient variation in the hardness of the soil, as measured by the penetrometer, to cause any great variation in the 'general population' of the shore. The cause of such local variations as do occur is discussed below.

THE LOCATION AND DISTRIBUTION OF THE LINES OF CASTINGS

A brief description of the shore zonation at Whitstable has been given by Newell (1948), and it will suffice to mention here that the lines of castings occur on the muddy sand of the Flats which stretches from within about 100 yd. of high-water spring tides nearly down to low-water mark, the lugworm belt varying in width from about 400 to 800 yd. The lines of lugworm casting are confined to an area of about 0.5 square mile, none being found east of Whitstable harbour nor west of the clay cliffs at Seasalter. The centre of the area in which the lines occur has a normal national grid reference of 097662 (sheet 173, 1 in. Ordnance Survey).

The lines were found to be of various lengths and widths but rarely exceeded 60 yd. in length or 2 ft. in width. Usually they were about 40 yd. in length and 18 in. in width. With practice the same line could be recognized on successive occasions, but, to test the permanence of the lines, five of them were marked by stakes when it was seen that they remained in a constant position during the period of 5 weeks over which they were observed.

Almost all of the lines were straight so that their magnetic bearings were easy to determine with a prismatic compass. The bearings of 50 lines were taken and are given in Table I.

Unaided observation gave the impression that the lines run at random in all directions, but it can be seen from the compass bearings recorded that there is

not an *equal* number of lines in all directions. More, in fact, occur with bearings of about 45° and about 165° than in other directions. The predominating direction of the lines of castings seems to be roughly parallel with the coastline.

TABLE I. BEARINGS OF LUGWORM LINES

Number of lines recorded in each 5° of arc, magnetic bearings.
Number of lines recorded in each 20° of arc is also indicated.

Bearing	No. of lines	Bearing	No. of lines	Bearing	No. of lines
0	1	60	2	120	0
5	2	65	0	125	1
10	1	70	1	130	1
15	3	75	1	135	0
20	3	80	0	140	3
25	0	85	0	145	1
30	2	90	1	150	2
35	0	95	1	155	1
40	4	100	1	160	3
45	5	105	0	165	2
50	1	110	0	170	0
55	4	115	0	175	3

POPULATION DENSITY OF THE LINES AND ADJACENT AREAS

The number of castings in the lines is greater than the number per square yard forming the general population of the shore. For example, castings on the shore which are not in lines vary in numbers from minima of 1 or 2 to maxima of 30 to 40 per sq.yd. The population of the lines may rise above 40 per sq.yd., whereas the areas adjacent the lines generally contain about 5 or 6 casts per sq.yd. To obtain these results areas of $\frac{1}{2}$ by 2 yd. were marked off, one on either side and one along the lines and the number of castings in each area was counted. The results are shown in Table II.

TABLE II. POPULATION OF LINES AND ADJACENT AREAS

Worms per sq.yd. flanking line	Worms per sq.yd. in line	Worms per sq.yd. flanking line
0	42	4
3	45	5
6	46	8
6	28	4
3	38	10
0	45	1
0	43	6
3	29	6
2	36	9
14	43	8

VARIATIONS IN SOIL DEPTH AND TYPE

As has been mentioned in previous papers, the soil of the Flats consists of muddy sand underlain by impervious clay. This stratum is almost certainly London clay (Dr J. F. Kirkaldy and Mr C. D. Ovey, private communications), and is found at different depths on different parts of the shore, being exposed near

low-water mark but being elsewhere overlain by a thickness of sand which varies from about 1 to 12 in. It has been noted that lugworms, which appear to be able to burrow and live in gravelly soil seem unable to penetrate the clay (Wells, 1945), or at least are not normally found living in it. Accordingly, the depth of the sand (or topsoil as it may well be called) was measured along the lines of casting by means of an auger and was compared with that in the less densely populated areas.

In each of four prominent lines a series of borings was made in order to record the depth of the topsoil (*a*) along the middle of the line, (*b*) at distances of 6 in. from the middle of the line, (*c*) at distances of 12 in. from the middle of the line, and (*d*) at distances of 18 in. from the middle of the line. A selection of these results is given in Table III, from which it can be seen that the topsoil is much deeper along the line than at its flanks.

TABLE III. DEPTH OF SAND IN AND NEAR LUGWORM LINES

Depth of sand in inches.						
18 in. from centre	12 in. from centre	6 in. from centre	Centre of line	6 in. from centre	12 in. from centre	18 in. from centre
8	9	10	12	9.5	6	8.5
7.5	8	12	12	10.5	7.5	6
4.5	7	11	12	5.5	3.5	3.5
5	10.5	15	12	11	10	4.5

THE GENERAL EFFECT OF THE DEPTH OF TOPSOIL ON THE NUMBERS OF WORMS

A close correlation between the dense population of lugworms and the depth of the topsoil along the lines of castings having been established it seemed of interest to find out if this principle were of wider application. Fortunately, a small area was found which showed patchy distribution of a different kind from that previously examined. In 1942 a large bomb fell on the Flats just seaward of the *Fucus* and shingle zone and, its crater subsequently filling with muddy sand, its presence was no longer detectable except for the extreme density of the lugworm population. The centre of the former crater had a great depth of topsoil, but was surrounded by a rim of clay covered merely by a few inches of sand. Within the margins of the crater the lugworm population had a density of 42 per sq.yd., that of the marginal zone being only 4 per sq.yd., whilst the undisturbed area outside the crater rim had a density of 28 per sq.yd. So sharp was the separation of an area rich in worms from an area practically devoid of castings that the counts from which the figures were quoted were made only a yard or so apart.

The evidence from the bomb crater and from a study of the lines of castings is strongly in favour of the view that one of the main factors influencing the density of the lugworm population is the depth of the topsoil overlying the clay rather than the admixture with the topsoil of even a large proportion of shingle or shell gravel.

MIGRATIONS OF THE LUGWORM POPULATION

There is some evidence in favour of the view that lugworms can change their burrows and that the population of a given area is not determined solely by the original settlement of the larvae. There are reasons for believing that movement to new burrows takes place through the water, that is by swimming. To test this view two pits, each a square yard in area, were excavated in the clay forming the rim of the former bomb crater, the clay being removed to a depth of 10 in. The pits were filled with topsoil from which an attempt had been made to remove all lugworms and were then examined occasionally for the

TABLE IV. REPOPULATION OF AN ISOLATED AREA OF DEEP SOIL

Date	No. of casts in marked square yard 1	No. of casts in marked square yard 2
	Pits dug in clay and filled with fine sand	
18 Aug. 1948	0	2
20 Aug. 1948	0	3
24 Aug. 1948	1	4
24 Sept. 1948	0	3
24 Oct. 1948	0	4
21 Nov. 1948	0	5
5 Dec. 1948	4	6
16 Jan. 1949	4	9
18 Feb. 1949	15	12
16 Apr. 1949	{16	{13
24 Apr. 1949	{13 headshafts	{11 headshafts

presence of worm castings. The number of castings found on visits made from the beginning of the experiment in August 1948 to April 1949 are shown in Table IV, from which it can be seen that the pits became repopulated gradually until the spring when there was a rapid immigration of worms. It is inconceivable that the worms could have burrowed through the very dense clay forming the walls of the pits. Neither were there, in fact, any worms to be found in the soil immediately adjacent to the pits, so that it must be concluded that they had repopulated the areas by swimming and burrowing from the surface.

From this it would seem that the patchy distribution of the worms, whether in lines or in other areas is due to the dynamic effect of a shifting population, the worms tending to aggregate in areas of deep topsoil most suitable to their burrowing and feeding activities. The explanation of the trenching in the clay, however, which allows of a deeper layer of topsoil is far from clear, but its solution must probably be sought in the geological history of the Flats. It is, nevertheless, interesting to find that the lugworm is a fairly reliable indicator of the depth of soil suitable to its (and probably to other animals') way of life, and that its discontinuity of distribution shows up, quite clearly, unsuspected discontinuities in what at first sight appears to be a very uniform habitat.

SUMMARY

It has been shown that the main factor which influences the local distribution of the lugworm at Whitstable is the depth of the muddy sand overlying the clay stratum below.

In places this clay is furrowed by straight channels which are revealed only by the arrangement of the lugworm castings. These are more numerous along the channels.

Migration of adult lugworms has been shown to occur, most freely in the spring.

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EXPLANATION OF PLATE 1

Figs. 1 and 2. Photographs of the muddy Flats at Whitstable showing lines of lugworm castings.



Fig. 1.

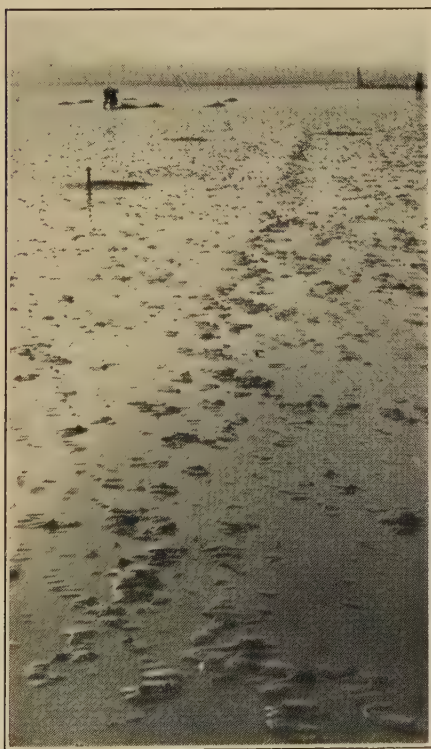


Fig. 2.

debris in suspension was caused to drain into the pit. The water in the pit was then poured, a pint or so at a time, through a small plankton net whose contents were then transferred at intervals to a jar of sea water. Usually about 20 gallons or so of sea water were filtered in this way, and the resulting suspension was then examined in Petri dishes for polychaete larvae. These were removed by means of a pipette and reserved for further examination. Trial and error soon showed that it was only in the pebbly *Fucus* zone that lugworm larvae were to be found and, it may be remarked, that it was only in this zone that the larvae of other polychaetes were at all plentiful.

DESCRIPTION OF LARVAE

Larva with three chaetigerous segments (Text-fig. 1)

On 17 November 1947, and 29 November 1948, larvae with three chaetigerous segments were found. Otherwise they differed but little in general appearance from larvae with two chaetigers previously described. Although able to swim by means of their cilia, they were usually enclosed in a layer of dense mucus. The prostomium was the largest division of the body and bore an apical tuft and one pair of eyes. A broad prototroch encircled the greater part of the prostomium and peristomium. The three segments behind the achaetous peristomium each bore a pair of dorsal chaetae and a minute crotchet. The dorsal chaetae were of two kinds; a capillary chaeta and a shorter one which was broadly winged or spatulate. Both neurotroch and telotroch were still prominent. The total length of the larva was 0.33 mm.

Larva with four chaetigerous segments

This was found on 14 November 1948. It measured 0.35 mm. in length and much resembled the three segment larva.

Early post-larval stage (Text-fig. 2 and Pl. 1, fig. 1)

An early post-larval stage was collected on 14 February 1949. Its total length when alive varied between 2.5 and 3.2 mm. and when fixed was 2.8 mm. with a diameter of about 0.4 mm. in the thoracic region. The tail was about half the length of the thoracic region from which it was sharply distinguishable by being narrower and achaetous. The prostomium, still a prominent lobe, bore six eyes, two of which were larger than the others and probably represented the single pair of eyes persisting from earlier stages. The otocysts in the peristomium were clearly visible in transparency and contained minute particles of sand.

Behind the peristomium were twenty segments bearing chaetae, but in the first chaetiger the chaetae, of which there was but one on each side, were difficult to detect. The next nineteen segments bore both notopodial and neuropodial chaetae. The notopodial chaetae (Text-fig. 3A) were of two kinds: (a) capillary with narrow wings, and (b) shorter ones with broad wings.

The neuropodial chaetae (Text-fig. 3B) were minute crotchets with a curved rostral hook and one (possibly two) smaller hooks. The number of crotchets varied from five in the second chaetiger to nine in the twentieth chaetiger.

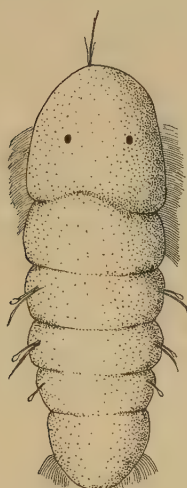


Fig. 1

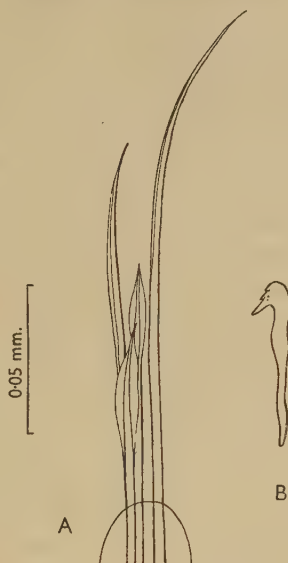


Fig. 3.

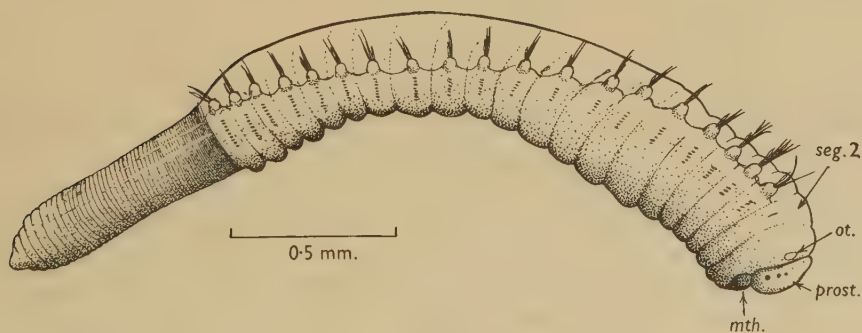


Fig. 2.

Text-fig. 1. Larva with three chaetigerous segments, dorsal view. $\times c. 175$.

Text-fig. 2. Early post-larval stage 2.8 mm. in length, side view. $\times c. 43$. *mth.*, mouth; *prost.*, prostomium; *ot.*, otolith; *seg. 2*, segment 2 (first chaetigerous segment).

Text-fig. 3. Notopodial chaetae from third chaetigerous segment (A) and crotchets from third chaetigerous segment (B) of 2.8 mm. post-larval stage. $\times c. 400$.

The tail consisted of about fifty segments and ended in a cone-like pygidium still bearing a trace of a telotroch. None of the segments of the body was as yet divided into annuli; neither were there any traces of gills. The gut was fully

functional and the worm seemed to feed by means of its eversible proboscis which engulfed food in much the same way as does that of the adult. Faecal matter was seen in the intestine and the food probably consisted of fine organic debris. The main regions of the gut, as well as the blood vessels, which contained blood with haemoglobin, were already differentiated. Nevertheless, the mode of life differed from that of the adult in that the larva was enclosed in a thick mucous tube, a good deal longer than the total length of the worm, instead of inhabiting a burrow excavated in the soil.

In fact, the smallest size of worm found living in the adult manner, as shown by the castings at the exit of the burrow, was 8 mm. in length. This figure is probably on the low side, owing to shrinkage during preservation and even larger specimens of up to 18 mm. in length, which were collected between 19 and 30 April 1949, were still living in mucous tubes like the earlier post-larval stages. Reference to Pl. I, fig. 2, will show that one of these specimens, which was 12 mm. long, has all the main adult features including the thirteen pairs of branched gills, annulation of the segments and papillae on the tail segments. Indeed, except in size, so closely does it resemble the mature worms that detailed description seems unnecessary.

Shortly after finding these specimens young worms began to make their appearance in the shoreward edge of the muddy sand flats which are the main habitat of the adults, and by 7 May 1949 their minute castings were seen in great profusion, indicating that seaward migration from the shore took place somewhat later in 1949 than in 1947.

DISCUSSION

Thorson (1946) figures a larva (fig. 59, p. 109) which he found in a mid-water bottle collector at Ven which he believes should be referred to *Arenicola marina*. It is true that his larva bears some resemblances to a young lugworm, but although it measured 2.8 mm. in length the two main regions of the body are not demarcated. It also differs from early post-larval lugworms collected at Whitstable in that: (1) there is no clear prostomium; (2) in the absence of capillary chaetae, all the chaetae apparently are crotchets; (3) there are twenty-one chaetigerous segments; and (4) despite the general lack of differentiation the segments are already marked off into annuli. When it is remembered that this larva was collected in the bottle between 27 July and 13 August, that is, at a time when Thorson states that the gametes are far from mature in the adult worms, it becomes reasonably certain that the larva was not that of *Arenicola marina* and may not even have been that of any species of *Arenicola*.

The 2.8 mm. post-larval stage from Whitstable also differs in several important respects from Benham's larva. Among these differences may be listed: (1) the general appearance; (2) the fact that Benham figures considerably fewer segments (about 30) in the tail region; (3) only two capillary chaetae are



Fig. 1. Photomicrograph of 2.8 mm. post-larval stage after clearing in cedar-wood oil. $\times c. 37.5$.

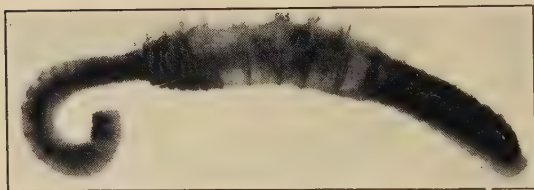


Fig. 2. Photomicrograph of late post-larval stage (12 mm. in length). $\times c. 7.5$.

figured in the anterior dorsal bundles, whereas, since Benham's larvae is much larger, even more bristles would be expected, not less; (4) the absence of notopodial lobes; (5) apparently the notopodial bristles are all of one kind, and (6) the smaller number of crotchets in the neuropodial regions.

Ashworth (1904) also succeeded in obtaining post-larval stages of *Arenicola*, but only when they were in the plankton. Reference to his descriptions and figures shows that they agree well with the older post-larval stages collected at Whitstable.

SUMMARY

Larvae with three and four chaetigerous segments and also an early post-larval stage of *Arenicola marina* are described with figures. These are all bottom-dwelling stages enclosed in mucous tubes and were collected from the pebble and *Fucus* zone at Whitstable.

The finding of these larvae furnishes additional evidence for the view that, except when migrating in the water to new habitats, the lugworm possesses no pelagic larval stage in its life history.

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THE MECHANISM OF OPENING AND CLOSING OF *CALLIACTIS PARASITICA*

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(Text-figs. 1-4)

INTRODUCTION

In a previous paper Chapman & Newell (1947) described the part played by the body fluid in the burrowing of the lugworm, and recorded the hydrostatic pressure occurring in the fluid contents of the coelom. The fluid-muscle system of this animal is completely closed, except for six pairs of nephridia which do not leak under pressures higher than those which occur naturally in the body of the worm.

It was considered of interest to inquire if the fluid-muscle system functions in the same way in an animal whose body cavity opens to the exterior by a wide aperture. *Calliactis parasitica* Couch was chosen as a large active animal whose normal or resting position is 'open'.

On the movements made by anemones, Hyman (1940) gives a few details of the method of working of the fluid-muscle system, but is obliged to quote Faurot's (1895) account of the burrowing of anemones into sand. Faurot describes only the outward appearance of the process in *Peachia* and says that 'il paraît évident que le liquide qu'elles renferment est soumis à une compression'. Jordan (1935) gives an analysis of the properties of *Metridium* body wall, but does not describe the working of the muscular system as a whole. He demonstrates that 'muscle preparations' can be stretched by very small forces and that they do not spontaneously regain their original length when the forces are removed, but he does not distinguish clearly between the properties of muscle and those of mesogloea. Pantin (1940) states that 'on stimulation most anemones cover the disk by contraction of the longitudinal retractors and the parietal muscles of the mesenteries. The mouth, disk and tentacles are pulled in, and during this process some water is squirted out of the mouth. Full re-expansion subsequently requires the gastral cavity to be filled again with sea water. This is done by ciliary action of the stomodaeum and is a slow process. In *Calliactis*, closure is due primarily to the contraction of a powerful sphincter at the edge of the column just under the tentacles. There is little loss of contained water and re-expansion depends simply on the comparatively rapid relaxation of this muscle'. According to Stephenson (1928), water may be lost at the cinclides, through which the acontia are carried by water currents.

He considers that the cinclides may function as safety valves in preventing rupture of the body wall.

From the foregoing it can be seen that there is room for an investigation into the mechanism controlling the volume of contained water and the origin of the restoring force which brings about the 'rapid relaxation' of the sphincter during the movements of *Calliactis*. It would seem that some light could be thrown on the way in which anemones move by the measurement of internal hydrostatic pressure during various phases of movement coupled with observation of their movements and some knowledge of the distribution of their muscular tissues.



Fig. 1. *Calliactis parasitica* fully open and fully closed.

OBSERVATIONS OF MOVEMENTS

When open, the tentacles of *Calliactis* are large, numerous, and well distended with water, and the disk is clearly displayed (see Fig. 1). On strong mechanical stimulation the animal can close rapidly and completely until its external surface is that of the column only (see Fig. 1). At the beginning of the contraction the tentacles diminish in size as their contents are expelled into the main gastral cavity, while the disk is retracted by the parietal muscles. A little later the powerful sphincter muscle at the edge of the disk just below the tentacles begins to contract so that the sides of the column are, as it were, drawn over the retracted disk until only a shallow depression indicates that the body wall is not continuous. The animal is now the shape of a bee skep and is firm to the touch, as if made turgid by the pressure of the muscular walls on the contained fluid. Even after strong stimulation this contracted posture

is not long maintained, the sphincter usually beginning to relax in less than 2 min. Relaxation of the sphincter is followed by the expansion of the tentacles which are inflated by the inrush of fluid from the enteron of the column.

It seems unlikely that expansion as rapid as that shown by *Calliactis* could be accomplished by means of water pumped into the enteron by ciliary action. As mentioned by Pantin (1940) there is little loss of contained fluid, as was seen by putting a few drops of carmine suspension on to the opening of the stomodaeum of an expanded anemone and stimulating it to contract. Only when the sphincter had nearly closed was there any suggestion that water had been ejected from the animal, and at that stage of the contraction it might well have come from the liquid squeezed out from between the retracted disk and the enveloping sphincter. Conversely, carmine applied to a closed anemone showed that very little water, if any, was taken in during opening.

In addition, carmine suspension was placed near to the cinclides at the base of the column. Neither on normal contraction, nor on contraction strong enough to extrude the acontia, was any water seen to leave the apertures, even as the acontia were being expelled. It is unlikely that *no* water escapes during the extrusion of the acontia, but the amount must be very small.

A test was made to see if water was lost at each contraction by an amount small enough to escape observation but sufficient, when lost repeatedly, to affect the speed of opening and closing. A small anemone was stimulated mechanically twenty-two times in the course of 1 hr. 40 min., and at the end of the period was opening and closing rather more rapidly than at the beginning. The creature was stimulated strongly enough to cause complete closure but not sufficiently to cause the expulsion of the acontia.

Since the animal appears to behave as a closed system analogous to that of *Arenicola*, the stomodaeum being closed during movement, it might well be expected that there would be some considerable variations in pressure during different phases of muscular activity.

THE INTERNAL HYDROSTATIC PRESSURE

An inclined capillary tube manometer filled with sea water was used to estimate the internal hydrostatic pressure, and was connected to the animal by a hypodermic needle of large bore. In use, the anemone formed the left-hand, and the capillary tube the right-hand, limbs of a manometer (see Fig. 2). Estimations were made by connecting the reservoir to the capillary tube until the level of the sea water in it rose to about 10 cm. above the level in the aquarium jar containing the animal. The tap was then turned so as to connect the anemone with the capillary tube and to cut off connexion with the reservoir. As preliminary tests had shown that less than 1 min. was required for the pressure in the animal and manometer to become balanced as shown

by a stationary meniscus, scale readings were made 1 min. after the animal was connected to the manometer tube. Control tests, made with the needle free in the water of the aquarium jar, gave a correction to be deducted from the scale reading which allowed for the height of the water in the jar and for the small capillary rise of liquid in the manometer tube above the level in the aquarium. Finally, the scale reading, made to the nearest mm., was halved, since the slope of the manometer was such as to give a multiplication factor of 2.

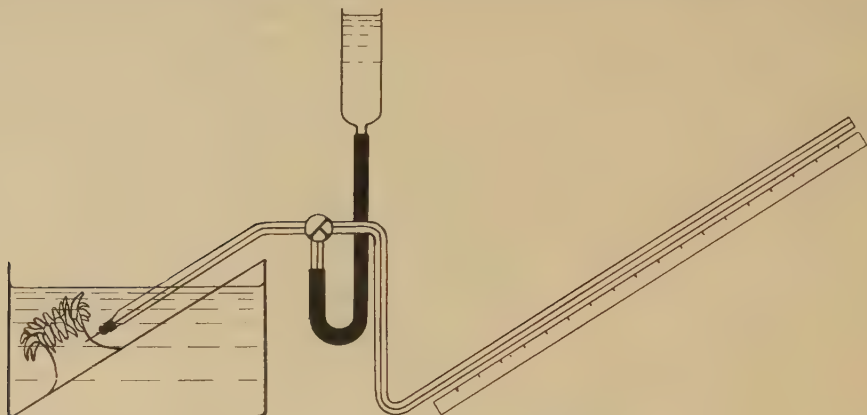


Fig. 2. Inclined capillary manometer.

TABLE I. MEAN PRESSURE IN CM. OF SEA WATER IN *CALLIACTIS*

Test no.	Expanded	Contracted
1	1.0	2.4
2	2.2	1.8
3	1.0	3.3
4	0.2	1.0
5	1.2	2.0
6	3.3	2.7
7	0.3	1.1
8	1.5	3.1

Several measurements were made on each animal both in the open and in the contracted state. Contraction was brought about and maintained by mechanical stimulation of the base of the column with a glass rod. Difficulty was sometimes experienced in keeping the animals contracted for a minute. The mean pressures measured by this method on the stock of eight animals are set out in Table I; detailed results are given in the Appendix.

The striking feature of Table I is the inconsistency of the readings, in spite of the fact that each figure represents a mean of between four and thirteen readings. Whilst, in general, the pressure in the closed animal is higher than it is in the open one, the amount of the difference is not constant, nor is the pressure in the open animals constant. A manometer was therefore made to

give a continuous indication of the pressure changes inside the animal without, however, providing an exact measure of the pressures recorded, in order to show whether the instantaneous pressures previously recorded are representative of the normal pressure range.

VARIATIONS OF THE INTERNAL PRESSURE

The apparatus, by which variations of internal pressure were shown (Fig. 3), consisted of a xylene-filled manometer connected to a very thin-walled rubber teat (*T*) at the end of a glass tube which could be manipulated and clamped with the teat in place in the enteron of the anemone. The air enclosed between the manometer and the teat could be put into communication with the

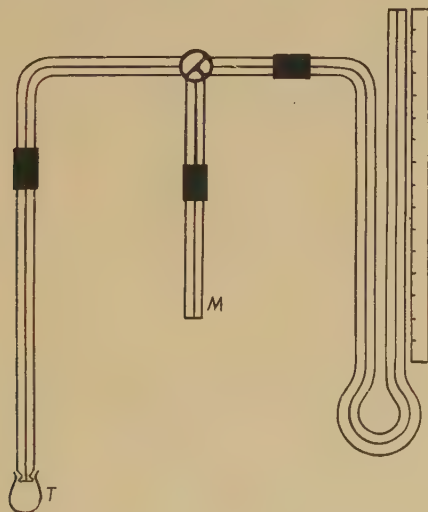


Fig. 3. Xylene-filled closed manometer. *T*, thin-walled rubber teat; *M*, mouthpiece.

exterior by a three-way tap, one position of which enabled the pressure within to be raised by blowing into it through a mouthpiece (*M*). The teat was made of rubber sufficiently thin to collapse when immersed in even 1 cm. depth of water, and hence was collapsed when it was quickly inserted into the stomodaeum of an open anemone. The glass tube bearing it was clamped into place and the teat was inflated by blowing gently into the mouthpiece until, at a pressure of 4 or 5 cm. of xylene, communication with the outside was cut off and the teat was left in communication with the manometer only. The apparatus was left for 5 min. to ensure that the air within the teat assumed the temperature of the water and hence remained practically constant during the course of the experiment. A scale was adjusted so that, at the beginning of the readings, the meniscus of the right-hand limb lay at zero. Readings of the pressure recorded by the manometer were made at 15 sec. intervals over

periods of up to 40 min. duration. From time to time the animal was stimulated by prodding the column with a glass rod, and throughout the experiment its state, whether open or closed, was recorded with the manometer readings. The times at which mechanical stimulation was applied, together with a line representing the state of opening of the animal, were marked on the records. The results of three typical tests are represented graphically in Fig. 4.

It will be realized that the pressures recorded by the manometer are not equal to the pressures occurring in the animal, but are the reaction of the resultant of three pressures acting on the wall of the teat. They can be represented diagrammatically:

$$\begin{array}{lcl} \text{Manometric pressure (} m \text{)} & \rightarrow & \begin{array}{l} \leftarrow \text{Pressure due to depth of submergence (} s \text{)} \\ \leftarrow \text{Pressure due to elastic deformation of teat (} e \text{)} \\ \leftarrow \text{Pressure due to anemone (} a \text{)} \end{array} \\ & & \text{Teat wall} \end{array}$$

At the beginning of the experiment when the scale is set so that the right-hand limb of the manometer is reading zero then

$$m = s + e.$$

When the anemone contracts and pressure is exerted on the teat due to that contraction then

$$m = s + a + e^1,$$

where e^1 is the new pressure due to elastic deformation at the new size of teat brought about by the pressure change occurring in the anemone. As a rises, therefore, the teat becomes less stretched, and e is therefore diminished. Since, however, e is small the pressure changes recorded by the manometer serve to show variations of the internal pressure of the anemone, even although they do not provide an accurate measure of them. No calibration or correction of the manometer was attempted, as it was considered that accuracy of pressure measurement was of less importance than indication of pressure change.

DISCUSSION

From these records it is clear why, in the previous tests, measurements of the internal pressures were inconsistent, particularly in the closed animal.

From inspection of the graphs, and from observations made during the course of the experiments, it would appear that, on mechanical stimulation followed by closure, pressure rises rapidly, generally attaining a maximum within 15 sec. This maximum pressure is developed only momentarily and immediately begins to fall, during which time the anemone may remain contracted or may begin to open again. With the beginning of opening either the rate of fall of pressure is briefly arrested or a small rise in pressure may

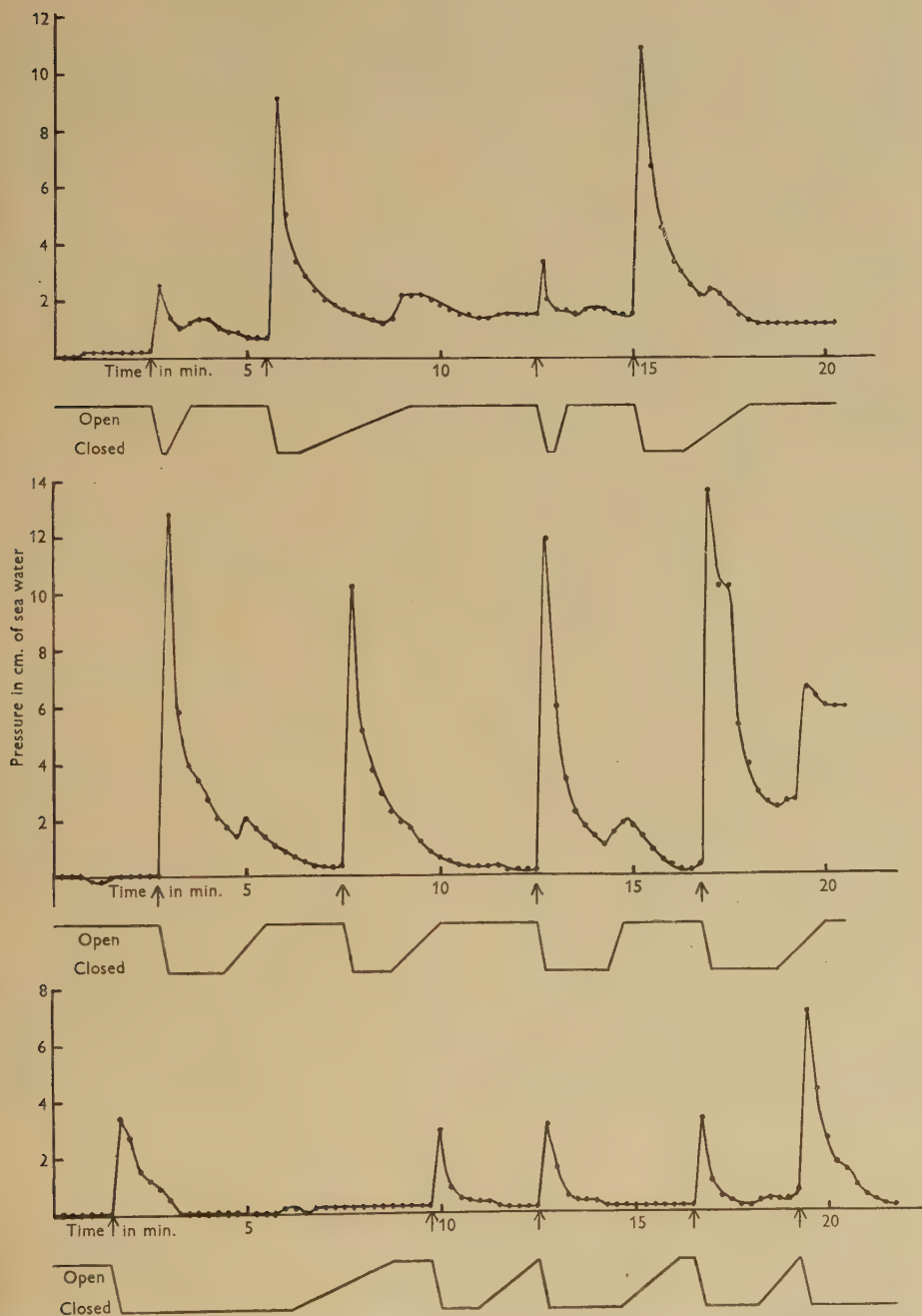


Fig. 4. Three records of the internal hydrostatic pressure changes in *Calliactis parasitica*. The animals were stimulated mechanically at the base of the column at the times marked by arrows; the line below each graph represents the opening and closing of the animal.

occur, followed eventually by a fall to the lowest pressures, which are recorded in the open animal. These variations in pressure are consistent with the properties of anemone muscle as described by Jordan (1935) and by Bozler (1936), and with the loss of very little fluid on contraction. Any loss through imperfect sealing of the stomodaeum would be reduced by a rapidly diminishing pressure.

The need for increased pressure on opening is connected with the arrangement of the musculature, which in *Calliactis* does not differ appreciably from the pattern described by Stephenson (1928) for anemones in general. The endodermal muscles comprise a circular layer which covers the foot, column, disk and tentacles, and from which the sphincter is derived as well as the muscles of the mesenteries (including the retractors of the disk), the parieto-basals and the basals. The ectodermal muscles, which are, in general, longitudinal, are absent from the foot and column (Pantin, 1935). On inspection, it can be seen that the contraction of any of these muscle layers, *in an animal whose body-cavity communicates freely with the outside*, would be to contract or to close the creature, diminishing the volume of water which it contains. The general arrangement of the musculature is such as would provide a satisfactory basis for movement in an *open* animal if the mesogloea were elastic, or if the creature acted as a *closed* fluid-muscle system.

As it had been shown that little, if any, water is lost on normal contraction, it was considered that the insertion of a tube into the stomodaeum did not upset the normal working of the animal sufficiently to invalidate the conclusions which have been drawn from the results obtained, namely, that during movements the animal behaves as a closed fluid-muscle system. The constancy of volume at which the animal works, and the slight rise in pressure which accompanies opening, suggests that although this may be aided by the physical properties of the mesogloea, it is due, at least in part, to the contraction of the circular muscles of the lower portion of the column. These alter the distribution of the enclosed water, constricting the column and expanding the disk and tentacles. It is true that the mesogloea of *Calliactis* is stronger than that of many other anemones and appears particularly so when cut out from the living animal. It is hoped that further work on the structure and physical properties of this material will enable a more exact estimate to be made of the amount which its elasticity plays in the movements of the animal.

SUMMARY

Experiments are described which suggest that *Calliactis* behaves as a closed animal in its movements, although its stomodaeum appears to be widely open to the exterior.

Observations of the movements of the animal are correlated with variations of the internal pressure. It is shown that expansion is not merely 'passive

relaxation', but is generally accompanied by a rise in pressure which is, however, much lower than that which accompanies rapid closing.

It is concluded that the fluid-muscle system of *Calliactis* behaves in a similar way to that of other soft-bodied invertebrates, but that the system works at a much lower pressure.

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APPENDIX

DETAILS OF PRESSURE MEASUREMENTS IN *CALLIACTIS*

Pressures are given in cm. sea water to nearest 0.1 cm.

All readings made 1 min. after connecting animal with manometer tube.

All readings are corrected for capillary rise, height of water in aquarium jar and for slope of manometer.

Anemone 1		Anemone 2		Anemone 3		Anemone 4	
Open	Shut	Open	Shut	Open	Shut	Open	Shut
1.4	1.2	2.9	0.5	0.7	2.3	0.3	0.6
2.3	3.1	3.0	1.5	0.9	5.0	0.2	1.1
1.5	1.6	1.0	1.6	0.9	2.1	0.2	0.4
0.8	3.7	2.9	2.0	1.1	3.7	0.1	0.9
0.8	2.5	0.9	1.7	0.8	4.5	0.2	1.4
0.5	—	3.4	1.9	2.1	1.9	—	1.0
0.3	—	0.7	3.2	1.3	—	—	1.5
0.3	—	3.6	—	0.7	—	—	—
—	—	1.2	—	0.6	—	—	—
—	—	—	—	0.9	—	—	—
Mean pressure	1.0 2.4	2.2 1.8	1.0 3.3	0.2 1.0			
Anemone 5		Anemone 6		Anemone 7		Anemone 8	
Open	Shut	Open	Shut	Open	Shut	Open	Shut
1.7	3.1	1.7	3.8	0.8	1.0	1.6	3.0
1.3	1.3	1.6	3.2	0.9	1.2	1.8	4.4
1.3	1.3	2.1	1.2	0.4	0.7	1.7	3.7
0.8	2.3	2.6	4.0	0.0	0.7	1.2	2.1
0.6	—	4.3	1.5	0.0	1.9	1.8	4.5
1.1	—	3.3	—	0.0	—	1.7	1.7
1.3	—	3.0	—	0.0	—	1.1	1.5
1.2	—	2.3	—	0.0	—	1.2	4.0
—	—	4.7	—	—	—	—	—
—	—	4.4	—	—	—	—	—
—	—	6.5	—	—	—	—	—
—	—	4.7	—	—	—	—	—
—	—	2.3	—	—	—	—	—
Mean pressure	1.2 2.0	3.3 2.7	0.3 1.1	1.5 3.1			

ON THE VOLUME MEASUREMENT OF WATER FILTERED BY A PLANKTON PUMP, WITH SOME OBSERVATIONS ON THE DISTRIBUTION OF PLANKTONIC ANIMALS

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INTRODUCTION

Winsor & Walford (1936) have suggested that variations in replicate vertical plankton hauls can be explained on a random distribution of the population which is affected by variations in the volume of water filtered, and the results of Silliman (1946) and Barnes (1949) are in apparent agreement with this suggestion. It might be expected that the use of a pump would eliminate such volume errors. Further, in view of the increased attention now being paid to the use of pumping methods for obtaining plankton samples, it is desirable to know the accuracy, under various conditions, of the volume estimation in such samples. The use of the pump has been described by Gibbons & Fraser (1937). Comparison of nets, pumps and the Clarke-Bumpus sampler has been given by Wiborg (1948).

THE ACCURACY OF FILLING A TANK

Various methods have been used for estimating the volume of water pumped, the simplest technique consisting of filtering the water through a net into a calibrated tank to a series of marks. This method has been used in this laboratory. An ex-National Fire Service pump fitted with 2½ in. armoured hose has been used, the water being pumped into a galvanized iron tank of dimensions 60 × 60 × 100 cm., i.e. a total capacity of approximately 400 l.

The volume of water pumped into this tank in any experiment was determined in the following way. After taking the sample a known volume of concentrated dye solution was added to the water and, after thoroughly mixing, a sample of the coloured liquid was taken and its transmittancy determined using the appropriate filters. The dilution was then obtained by reference to a calibration curve for dilution and transmittancy. The transmittances were determined by means of the Spekker Absorptiometer using 20 cm. cells. It was necessary to construct a calibration curve each day using the water pumped on that occasion since the amount of suspended matter and organisms in the water, contributing to the absorption, varies from day to day. The accuracy of such volume determinations was approximately ± 1 l.

The procedure was as follows. Having adjusted the pump throttle and valve (see p. 654) to deliver water at an approximately known rate, the person in

charge of the delivery hose filled the tank to a mark and removed the hose. As the water level approached the mark the hose was raised so that it could be quickly moved clear of the tank when the desired level was reached. At the same time the water delivered at the pump by-pass was collected and measured in a measuring cylinder (see later for discussion). After filling up to a mark in this way, the concentrated dye solution was added to the water in the tank, and after stirring a subsample was taken. This was repeated several times, the tank being carefully washed out with the hose between each experiment. The transmittances of the samples were then determined and the volumes of water taken in the tank calculated. Results of the first series are given in Table I. (The results given in Tables I-III were obtained with the engine running continuously throughout each series.)

TABLE I. FIRST PUMP SAMPLES TAKEN ON PIER

Nominal volume taken, 200 l.; weather rather cold, little wind; pumping speed approximately 200 l./min.

	Volume (l.)	Volume, by-pass (ml.)
	204	3543
	206	3510
	205	3517
	192	3548
	200	3591
	191	3638
	190	3600
	201	3622
	190	3641
Mean	197.7	3579
Standard deviation	6.8	51
Coefficient of variation (%)	3.4	1.4

The factors influencing the accuracy with which the required volume is obtained, when attempting to fill a tank up to a mark in this way, are the judgement of the person manipulating the hose, particularly in relation to movement of water in the tank, and his efficiency in removing the hose after the mark has been reached. With practice one tends to allow for the small amount added during the removal of the hose. Any change in the speed of pumping will affect the accuracy by its effect on these two factors. It is evident from the results that under these working conditions the volume of water by this method can be taken with reasonable precision and that the variations are very much less than those encountered in plankton sampling.

In the second experiment the pumping speed was increased and the same number of samples taken.

The greater pumping speed increases the motion of the water in the tank and gives more foam on the surface, both factors tending to make the estimation of the point at which the mark has been reached more difficult. The error due to water being added whilst removing the hose is also increased. However,

even with these possible sources of increased errors and under slightly more adverse weather conditions the accuracy of the volume measurement is unchanged. It should be noted that high pumping speeds are undesirable in collecting plankton since they may lead to the washing of material through the net, and to damage of the collected material.

TABLE II. SECOND PUMP SAMPLES TAKEN ON PIER

Nominal volume taken, 330 l.; weather, cold with some wind; pumping speed approximately 350 l./min.

	Volume (l.)	Volume, by-pass (ml.)
	332	1569
	331	1589
	324	1573
	324	1572
	344	1579
	340	1567
	340	1581
	326	1559
	306	1547
Mean	330	1571
Standard deviation	11.5	12.4
Coefficient of variation (%)	3.5	0.8

The above experiments were repeated on board ship.

Here judgement in filling up to the mark is very considerably hampered by any movement, which if the tank is filled to the higher marks may even result in loss of water.

TABLE III. PUMP SAMPLES TAKEN ON BOARD SHIP

Nominal volume taken, 200 l.; weather, some wind, fairly cold; pumping speed approximately 150 l./min.

	Volume (l.)	Volume, by-pass (ml.)
	219	3375
	199	3380
	195	3295
	195	3420
	197	3380
	181	3440
	186	3350
	200	3375
	206	3425
Mean	197.6	3382
Standard deviation	11.0	43.8
Coefficient of variation (%)	5.6	1.3

Although the error in the measurement of the volume is still quite small it is greater than at double the pumping speed on shore, and with increasing adversity of weather conditions the error of volume measurement on board might be expected to increase rapidly. It should also be noted that during the experiments described no net was used and no material was collected; attention could therefore be focused entirely on filling the tank.

CALIBRATION OF THE BY-PASS

On ship, however, even under good weather conditions, the use of tanks can hardly be said to be a convenient technique of volume measurement, since for continuous work two rather cumbersome tanks taking up considerable deck space must be employed, one to be emptying whilst the other is in use. Consideration was given, therefore, to other possible methods of volume measurement. With a pump running at constant speed the timing of the delivery, once it was calibrated (and if checked at intervals) would be satisfactory when using a constant length of hose. However, even with constant hose length, this is not possible with the type of pump in use here, since the rate of delivery is determined both by the position of the main valve and by the engine speed, the latter being controlled by a throttle whose setting cannot be accurately reproduced from day to day.

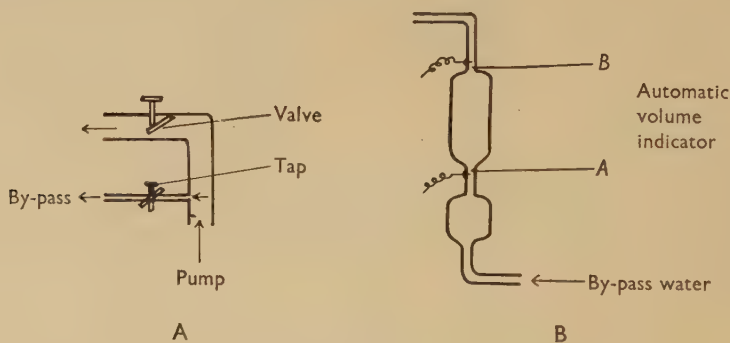


Fig. 1.

It was therefore decided to determine whether the volume of water going through the by-pass (used to cool the engine) could be used as a measure of the volume pumped. This by-pass water is taken through a filter fitted with a cock which can be conveniently used to take a sample. The amount of water forced into the by-pass depends both upon the position of the main valve (which as it is closed causes considerable back pressure) as well as upon the engine speed. At a given engine speed the volume of by-pass water increases as the valve is closed and therefore as the volume pumped decreases. The arrangement is indicated in Fig. 1A.

The results already given (Tables I-III) show that at a given engine speed and main valve position the amount of water delivered from the by-pass was constant for a constant volume collected (within the limits of error of the latter), and under these conditions the error in the volume of by-pass water is not greater than the error in filling the tank. The factors contributing to the errors of the two estimates of volume pumped are not identical; in taking the by-pass water co-ordination with the person working the hose is of importance for accurate work. That the coefficient of variation of the by-pass volume is

less than that of the tank volume suggests that the co-ordination between the two workers was excellent and that much of the error in taking the tank volume is due to the water added when putting in and taking out the hose, since the by-pass water was taken when the person working the hose gave a shout at the beginning of the experiment and when the mark had been reached, and since manipulation of the vessel collecting the by-pass water was simpler than removal of the hose.

That a constant by-pass volume was obtained for other valve positions and engine speeds is shown by the results in Table IV. The actual volume delivered was not measured in these experiments, but the tank was filled up to a mark.

TABLE IV. BY-PASS VOLUMES FROM PUMP SAMPLES AT DIFFERENT VALVE POSITIONS

Samples taken on pier; nominal volume taken, 330 l.; weather, cold with some wind; pumping speed approximately 330 l./min.

Main valve position...	2 turns	3½ turns	4 turns
	Volume (ml.)		
	1361	1366	1465
	1273	1340	1475
	1304	1356	1528
	1356	1354	1453
	1354	1338	1396
	1352	1326	1394
	1264	1311	1360
	1273	1320	1406
Mean	1317	1339	1435
Standard deviation	44.5	19	55
Coefficient of variation (%)	3.4	1.4	3.8

Note. These experiments were not done on the same day. The engine speeds would be different, which accounts for similar volumes being obtained with different values of cock position used.

Under given working conditions of fixed valve position and fixed running speed a satisfactory calibration could therefore be obtained between volume of water pumped and by-pass volume. The main valve position is readily reproduced and maintained but a given engine speed is difficult to reproduce. However, with fixed valve position it might be expected that for *small* changes in engine speed the by-pass water would be constant for a constant volume pumped, i.e. changes in engine speed would affect both volumes of water in the same proportion. Table V gives some results of experiments with varying engine speeds at two fixed valve positions.

For small changes in engine speed, at fixed positions of the valve, the delivery at the by-pass is a satisfactory measure of the volume pumped. A calibration of the pump is therefore possible in terms of the by-pass water. After calibration it would then only be necessary to measure the by-pass water in order to compute the volume of water pumped at a given valve position and engine speed. This by-pass water could be collected in a measuring cylinder.

In order to ensure that the engine speed is approximately constant throughout any given series the preliminary adjustments have been made with the aid of a simple pressure-measuring device, utilizing the pressure developed in an upright tube at right angles to the direction of flow. As a pressure meter an ex-R.A.F. rate-of-climb indicator has been used. As supplied it records rate of change of pressure, but if the air escape is blocked then actual pressures are recorded in arbitrary units and the instrument is then far more sensitive than the similarly constructed altimeters or air speed indicators. This was attached to one of the two similar paired cocks on the by-pass filters (only one of these

TABLE V. BY-PASS VOLUMES AT DIFFERENT ENGINE SPEEDS
(AT TWO VALVE POSITIONS)

Samples taken on pier; nominal volume taken, 330 l.; weather, good; pumping speed approximately 330 l./min.

Main valve...	2 turns		4 turns	
Throttle	Volume (ml.)	Mean volume	Volume (ml.)	Mean volume
(a)	1955 } 1937 } 1938 } 1928 }	1940	1392 } 1391 } 1405 } 1406 }	1399
(b)	1886 } 1920 } 1931 } 1919 }		1396 } 1389 } 1401 } 1377 }	
(c)	1918 } 1910 } 1932 } 1930 }		1348 } 1333 } 1344 } 1343 }	
(d)	1826 } 1846 } 1835 } 1836 }		1282 } 1295 } 1280 } 1289 }	
	1919 } 1898 } 1889 } 1925 }	1908	1170 } 1181 } 1220 } 1215 }	1197

(a), (b), (c) and (d) represent very considerable successive increases of engine speed which are, however, different in the two separate experiments since the position of the main valve varied (2 turns and 4 turns).

cocks can be used at the same time; a simple valve allows transfer from one to the other), the second being used to collect the water. A fixed position is necessary and metal tubing and metal unions were used for connexions both to the cock and to the pressure meter.

It was shown that when the pressure was adjusted by means of the throttle to a given value as indicated by this meter a constant volume of water was pumped (at constant main valve position, which is readily reproduced). That this is so is indicated by the results given in Table VI.

Collection of the by-pass water, followed by measurement of its volume in a cylinder, is not very convenient, although a good deal more so than the use of two large tanks, and a device has therefore been made which gives a signal when a known volume of water has been delivered. This consists of a vessel (Fig. 1B) with a large and small section connected to the by-pass cock and having platinum electrical contacts at the entrance and exit of the main bulb. The small lower bulb serves to delay the first contact after the by-pass water has been turned on, thus giving the person working the hose time to get ready. The contacts are

TABLE VI. BY-PASS VOLUMES AT DIFFERENT PRESSURES

Samples taken on pier; nominal volume taken, 330 l.; weather, good; constant main valve position; pressure changed by changing engine speed.

Pressure (arbitrary units)	Volume (ml.)	Mean volume (ml.)
5.2	2526	2537
	2527	
	2558	
6.6	2760	2768
	2775	
7.8	3586	3585
	3543	
	3626	
5.2*	2480	2492
	2512	
	2483	
	2495	
	2514	2511
	2508	
	2512	
	2504	2528
	2458	
	2565	
	2618	
	2493	

* Between these three series the cock was moved and readjusted and the pressure meter taken down and reassembled.

connected to a thermionic relay in circuit with a bell. Contact is made immediately the water reaches *A* and the bell rings; the circuit is then broken by means of a switch, which puts the second contact in circuit, and the bell rings again when the water reaches the second contact at *B*. The person working the hose collects water between the ringing of the first and second bells.

Using this device the volume of water in the tank can be accurately and conveniently taken. The volume pumped for a fixed volume of the by-pass (i.e. volume of large bulb) with fixed valve position and approximately constant engine speed (adjusted by pressure meter) can be varied by inserting a tap at the inlet to the lower bulb. However, in view of the possibility of such a tap slipping and since in general only a small number of different units of volumes are likely to be required at one period in this type of work, a series

of interchangeable tubes of varying bore have been used between the by-pass delivery (kept with cock fully open) and the entrance to the apparatus.

Using this method the results in Table VII were obtained. The apparatus was dismantled between the three runs which were done at intervals of several days, the volume being measured by the method already outlined. Once calibrated (which can be done on shore) the apparatus may be used to collect known volumes of water without the use of large tanks. A small vessel into which the collecting net can be held is used, the net being kept under the water during filtration.

TABLE VII. VOLUMES IN TANK FOR FIXED BY-PASS VOLUME

Nominal volume taken 200 l.; weather, good on shore, only moderate on ship; pumping speed approximately 170 l./min.; separate days' experiments.

Pump standing on pier, volume (l.)		Pump on ship, volume (l.)
197	190	190
191	186	187
189	200	189
189	196	192
194	197	195
196		191
Grand mean		192.3
Standard deviation		4.0
Coefficient of variation (%)		2.1

THE RESULTS

If the assumptions of Winsor & Walford are correct, samples taken by a calibrated pump should show considerably less variation than net samples. So far only a small number of samples have been taken and analysed. In the first series of experiments approximately 1000 l. were pumped for each sample and four consecutive samples were taken. The total time to take one sample was of the order of 6 min. (170 l./min.), and allowing for the time taken in changing the nets and bottling off the catch the whole collection occupied about $\frac{3}{4}$ hr.

The net was a small fine net (200 meshes to the inch) held in a tank of water with the whole of the filtering surface immersed whilst the water being pumped was, as far as possible, not directed on to the net surface.

Four samples were taken, and since the collections took a considerable time they have been grouped in two pairs and the results of the analysis of variance

TABLE VIII. COMPOSITION OF PLANKTON SAMPLES FROM
FOUR CONSECUTIVE PUMP HAULS

Group	Haul			
	1	2	3	4
Nauplii	2662	2142	2200	2166
Copepodites	485	466	565	833
Lamellibranchs	608	882	1118	1279

are given below. In each sample three groups of organisms were counted, namely, copepods (adult stages), copepods (nauplius stages) and lamellibranch larvae (Table VIII).

Analysis of the variance¹ of these data gives the following results:

	Degrees of freedom	Sum of squares	Mean squares
Main effects:			
Groups	2	0.7441	0.3721
Hauls	1	0.0062	0.0062
Times	1	0.0370	0.0370
First-order interaction:			
Groups-hauls	2	0.0142	0.0071
Groups-times	2	0.0351	0.0176
Hauls-times	1	0.0025	0.0025
Second-order interaction:			
Groups-times-hauls	2	0.0109	0.0055
Totals	11	0.8500	

The values for the times, group-haul, group-time and haul-time interaction are not significant. There is, therefore, no significant change in population, and the analysis can be simplified and regrouped as follows (this is equivalent to treating the data as four consecutive hauls):

	Degrees of freedom	Sum of squares	Mean square
Groups (G)	2	0.7441	0.3721
Hauls (H)	3	0.0457	0.0152
Residual	6	0.0602	0.0100

The mean square for the hauls is not significant.

σ_{GH}^2 is a measure of the within-haul variance

$$\sigma_{GH}^2 = 0.0100.$$

Standard deviation = $\sigma_{GH} = 0.1000 = \log 1.259$, corresponding to a coefficient of variation of 25.9%.

A further pair of hauls gave 21% as the coefficient of variation of a single observation, the conditions being similar to those of the first series.

These results indicate that little improvement has been effected by the use of the pump, and a third pair substantiated these results. It was thought that the manipulation of the catch on board was a possible source of error, and in a fourth series a pair of nets was used for the filtration. Two samples were taken of 220 l., the total time between beginning the first haul and completing the second being less than 10 min. These nets were new and 'identical' and were soaked for some time before use. After filtering the pumped water, the nets were carefully transferred to buckets without removing the collecting bucket and taken to the laboratory where the catch was removed with extreme

¹ Logs of catches have been used. The hauls have been separated into Haul 1 and Haul 2 since there is some evidence that the first haul of a series is different from the second, due to the state of the net. The above results do not substantiate this suggestion.

care using a fine jet to wash down the catch. A large number of species were counted and thanks are due to Dr S. M. Marshall for counting this set. The analysis of the variance of the data yields the following:

	Degrees of freedom	Sum of squares	Mean square
Hauls (H)	1	0.1122	0.1122
Species (S)	54	56.2223	1.0412
Interaction	54	0.6787	0.0126

Thus $55\sigma_H^2 + \sigma_{HS}^2 = 0.1122$,

and $\sigma_{HS}^2 = 0.0126$.

Hence, $\sigma_H^2 = 0.0018$,

corresponding to a standard deviation of $0.0424 = \log 1.103$, giving a coefficient of variation of 10.3%.

Further, $\sigma_{HS}^2 = 0.0126$,

or a standard deviation of $0.1123 = \log 1.295$, corresponding to a coefficient of variation of 29.5%.

The standard deviation of a single observation is

$$\sqrt{(\sigma_H^2 + \sigma_{HS}^2)} = \sqrt{0.0144} = 0.12 = \log 1.318,$$

corresponding to a coefficient of variation of 31.8%.

TABLE IX. THE DISTRIBUTION OF χ^2 DERIVED FROM POISSON SERIES (AS EXPECTED ON A RANDOM DISTRIBUTION), AND NET AND PUMP SAMPLES FOR ALL ORGANISMS

χ^2 value	Poisson	Nets	Pump
0.00039	5	4.5	5.5
0.0158	5	1.5	3.6
0.0642	10	3.7	3.6
0.148	10	5.2	9.1
0.455	20	10.4	9.1
1.074	20	11.2	5.5
1.642	10	9.0	12.7
2.706	10	11.9	7.3
3.841	5	11.2	3.6
> 3.841	5	31.3	40.0

DISCUSSION

The results from this small series of pump samples do not show any less variability than found with the net samples, and their similarity is confirmed on comparing the values of χ^2 for the two series. In the distribution of χ^2 , and in the relation between χ^2 and sample size, the two series show similar trends as shown in Tables IX and X, in particular the fact that even with pump samples the large values of 'sample size', i.e. population density high, contribute a very large proportion of the abnormally high discrepancies. Doubt is

therefore cast upon the assumption that the variability of net hauls is due to variation in the volumes of water filtered, since this was controlled in the pump samples, and it seems desirable to re-examine the assumption that the animals are randomly distributed, since it was upon a random population that variable volume filtered was supposed to act. Work designed to investigate the distribution of the organisms, using a new method of sampling, is already in progress.

TABLE X. SUM OF χ^2 BY SAMPLE SIZE (POPULATION DENSITY)

Numbers in brackets indicate number of samples in each group.

	Net	Pump
5-40	128.928 (50)	8.598 (12)
40-170	100.513 (44)	65.401 (19)
170-400	69.076 (19)	51.699 (7)
400-1000	161.507 (9)	128.690 (11)
> 1000	1726.151 (12)	227.718 (6)

I wish to thank Dr R. Robb for his criticisms and to acknowledge the help of Mr R. Kerr and Mr C. Davidson in the experimental work.

SUMMARY

The accuracy of volume estimation in filling a marked tank by means of a plankton pump has been determined. The method even in its simplest form is satisfactory under good conditions. Further refinements, in which the plankton was filtered off, after filling a modified tank (for example with an overflow device) would no doubt increase the accuracy.

A device is described by which, using an ex-N.F.S. pump, a constant (but variable by selection) volume of water can be taken without the use of large tanks.

A small number of sets of samples taken with adequate volume control indicate the same order of variability as net hauls. Comparison of the distribution of χ^2 for paired samples with nets and pumps also indicates variation of a similar type.

These results suggest that the variability of net hauls is not entirely due to the variations in the volume of water filtered. Further work is in hand to elucidate this question.

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AN APPARATUS FOR PRODUCING ARTIFICIAL TIDES

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From the Plymouth Laboratory

(Text-figs. 1-2)

It is often desired to grow animals and plants of the intertidal zone in the laboratory, under conditions as far as possible simulating those in nature and with the least trouble and expense. This need was felt by the writer during an ecological study of the diatoms inhabiting the mud-flats at Whitstable, Kent. It was found necessary to maintain such diatoms in the laboratory in London in a healthy condition for several days so as to study the effect of light and tides on their movements. The apparatus described in this paper was therefore devised. It has an advantage over other tidal systems (Bracher, 1919; Martin & Reid, 1935) in that the substratum could be automatically alternately flooded and drained at regular intervals by a much simpler mechanism. Besides, it is more handy and can be operated with only a small supply of sea water, a matter of some importance in localities remote from the sea.

It consists of a tidal chamber, T , and a reservoir, R (Fig. 1). The former is an inverted bell-jar fitted with a rubber bung through which passes a long glass tube, g , which extends to the base of the reservoir. At the upper end of the tube is a small funnel by which sea water enters the apparatus. A T-tube, t , serves to connect the tidal chamber and reservoir, its horizontal arm being connected to the siphon S .

The wide-mouthed bottle constituting the reservoir is fitted with a stopcock, v , which is useful for expelling air when setting up the apparatus.

The mud with the diatoms, m , is held in a container, w , of fine-meshed wire gauze covered with a few layers of muslin to prevent the mud from slipping through. The tube, g , passes through the centre of this container which rests on supports so that the upper surface of the mud is at a level about half-way up the bell-jar. The chamber T can be covered with a sheet of glass, and fitted with a thermometer, but this must of course not make an air-tight fit.

When in use, sea water is allowed to drip into the funnel from the jet of the constant delivery device shown in Fig. 2. This ensures that the rate of delivery shall be the same irrespective of the level of the water in the aspirator since the pressure head remains constant, being determined only by the height, x (Fig. 2). Any air-bubbles remaining after the reservoir has been filled are

allowed to escape through the stopcock, v , which is then closed. The water now passes up the tube, t , simultaneously in the tidal chamber and the siphon-tube. When it reaches and covers the surface of the mud in the chamber a condition somewhat comparable with that of high tide is realized and persists until the water reaches the level l . The siphon then commences to discharge water from the tidal chamber much more rapidly than it flows in and this continues until the chamber and siphon are emptied. Water then rises again in the tidal chamber

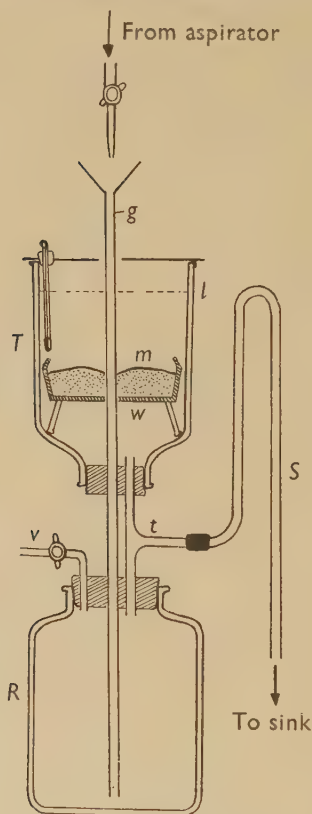


Fig. 1. Tidal apparatus (for description see text).

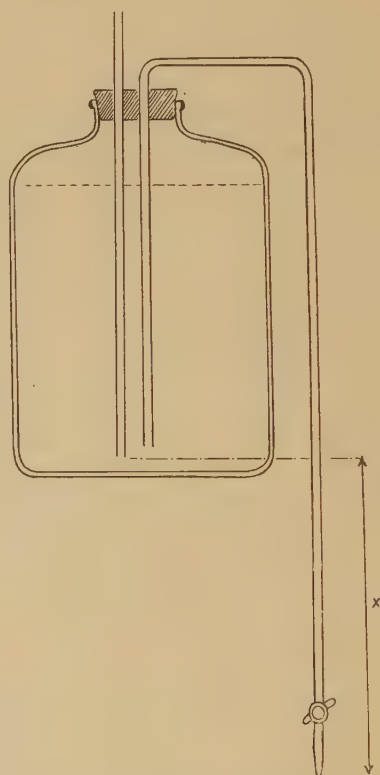


Fig. 2. Aspirator supplying the apparatus with a constant flow of sea water.

and the same succession of events is repeated. This will go on automatically for an indefinite period.

The rate of dripping, the position of the wire container holding the mud, the height of the level l , and the rate of discharge through the siphon can all be adjusted so that the mud surface is subjected to two periods of submergence and two periods of exposure in each 24 hr., with an interval of 6 hr. between successive phases. The bore of the siphon-tube is such that the discharge of

water from the chamber occupies only a minute or so. The rate of supply can be adjusted by means of a tap so that longer or shorter periods of exposure or submergence of the mud can be obtained. Moreover, the effects of different factors on the movements of the diatom community can be compared by using several similar pieces of apparatus fed from a common supply of sea water.

The apparatus could be used for maintaining animals and plants of the intertidal zone in the laboratory or for studying the effects of exposure on the growth of algal germlings (*Fucus*, *Laminaria*, etc.). The mud would then be replaced by an appropriate substratum.

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THE LAST LARVA AND POST-LARVA OF *TYPTON SPONGICOLA* FROM PLYMOUTH (CRUSTACEA DECAPODA)

By Marie V. Lebour, D.Sc.

From the Plymouth Laboratory

(Text-figs. 1-4)

The first larva of *Typton spongicola* was described in 1925 from the eggs carried by the parent (Lebour, 1925). No later stages are known; therefore it was interesting to find a last larva in the plankton from 2 miles north-east of the Eddystone (21 August 1946), which changed to the post-larva in the laboratory. There seems to be no doubt that the identification is correct although, surprisingly, the antennal scale, rudimentary in the adult, is still large. The agreement in colour of the last larva and post-larva with the newly hatched first larva, and the great similarity in the structure, in most ways, of post-larva and adult, makes it practically certain that we are dealing with *T. spongicola*.

A specimen of a post-larval *Typton*, almost certainly *T. tortugae*, was found in one of Dr Hilary Moore's hauls from Bermuda in 1940. This is much smaller than the Plymouth post-larva, but a good deal further advanced, having no antennal scale, and is interesting for comparison with *T. spongicola*.

Typton spongicola Costa (Figs 1-3)

The Last Larva

The last larva measured *c.* 4.8 mm. in length, but it is difficult to be exact because of the internally bent body, the abdominal hump coming up close to the head and the legs bent up parallel to the body, the antennules and antennae held straight out. This is distinctly of the *Mesocaris* type (see Gurney, 1938; Gurney & Lebour, 1941), with the body doubly flexed and legs 3-5 equal or sub-equal and not elongated. The colour is deep orange with red spots, most of the sixth abdominal somite, telson and uropods colourless, agreeing with the colour of the first larva. The animal makes sideway leaps in much the same way as do so many of the hump-backed larvae of similar form, so numerous in the Bermuda plankton. There are setose exopods on legs 1-4, but not on 5, leg 5 being very slightly longer than legs 2 and 3. This larva changed to the post-larva in the laboratory (26 August 1946), and the following description is taken from the cast skin. The rostrum is short and pointed with one spine

dorsally. The carapace has a small supra-orbital spine and a short spine probably to be regarded as antennal, and there is a point at the outer anterior angle. The abdominal somites are rounded, the sixth being very long, longer than 2-5 combined, the uropods slightly pointed, the telson long with one

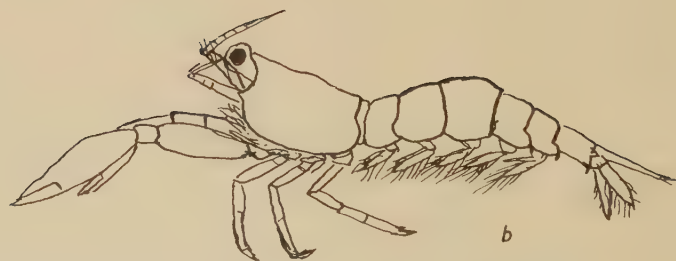


Fig. 1. *Typton spongicola*. Sketch from life of (a) the last larva, (b) the post-larva from last larva.

pair of lateral spines and 8 terminal setae, the outermost the longest, the third from the outside next in length, the inner setae very short. The antennule has two short branches, a tooth on the outer margin of the base and a small tooth near the centre of the basal segment. The antenna has a short segmented flagellum and a well-developed scale. The mandible has a grinding and

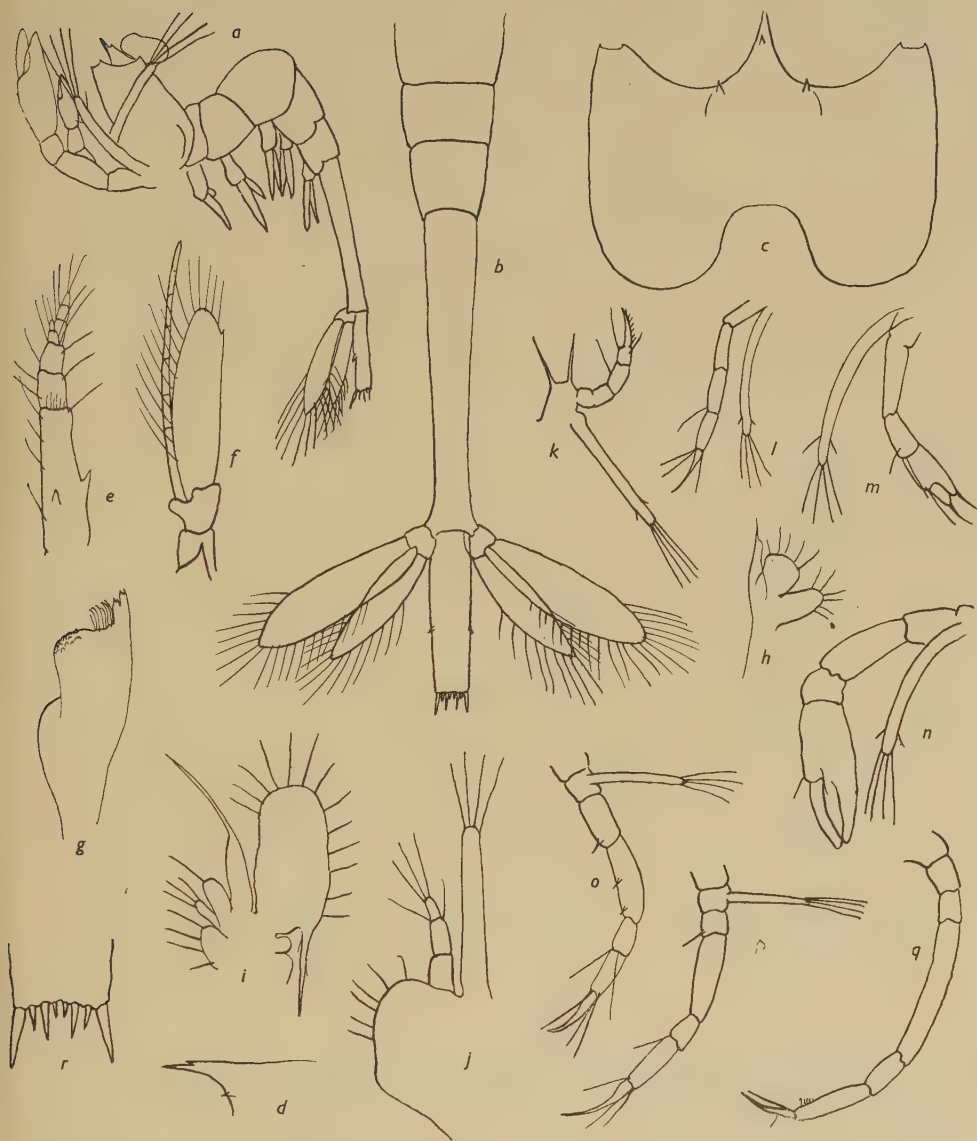


Fig. 2. Last larva of *Typton spongicola*: a, cast skin of body; b, abdomen and tail fan; c, carapace; d, rostrum; e, antennule; f, antenna; g, mandible; h, maxillule; i, maxilla; j, first maxillipede; k, second maxillipede; l, third maxillipede; m, first leg; n, second leg; o, third leg; p, fourth leg; q, fifth leg; r, end of telson.

cutting edge, the maxillule with two inner setose lobes and an endopod with a terminal seta. The maxilla has setae all round the exite, three inner setose lobes with 1, 3 and 4 setae respectively, and an endopod without a basal lobe and with a long terminal seta. The first maxillipede has a broad setose base, an endopod with three segments and 5 setae and an unsegmented exopod

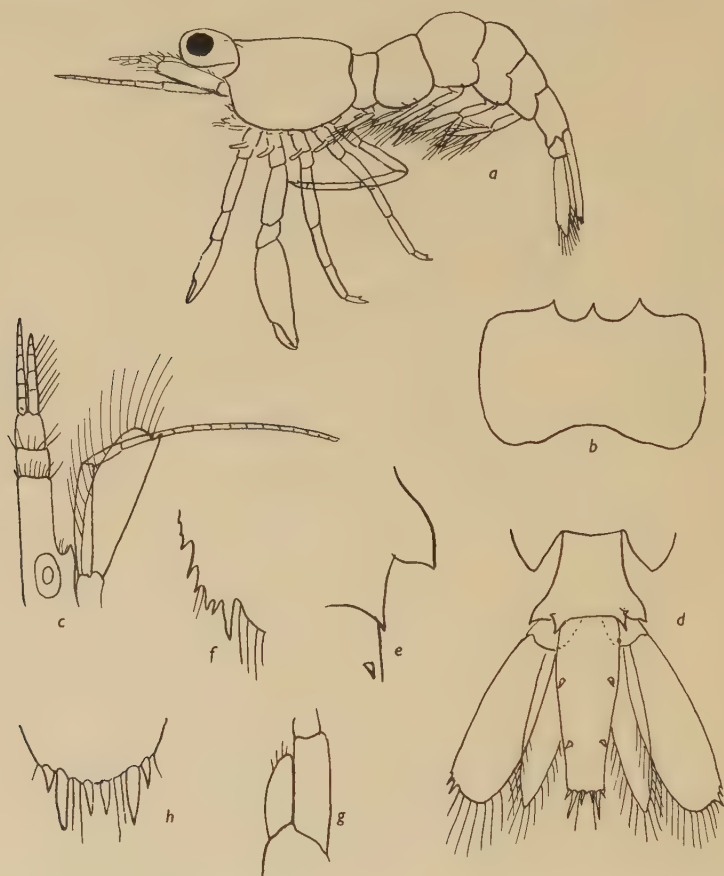


Fig. 3. *Typton spongicola*. a-d, post-larva from last larva: a, side view; b, carapace; c, antennule and antenna; d, telson and uropods. e-h, adult: e, end of last abdominal somite; f, outer angle of uropodal exopod; g, rudimentary antennal scale; h, end of telson.

with 4 setae. The second maxillipede has a broad base with 2 strong setae, a 4-segmented endopod ending in a strong hook and an unsegmented exopod with 6 setae. This strongly resembles the second maxillipede in the first stage, as does also the third maxillipede, the endopod of which ends in a strong claw with stout setae at the base. The first leg has an exopod with 6 setae and a chelate endopod; the second leg is similar but longer with a larger chela;

the third and fourth legs are sub-equal with 4 setae on the exopod, the endopod ending in a long pointed dactyl; the fifth leg is slightly longer and without an exopod. There are no setae on the pleopods.

The Post-Larva

The Post-larva from the last larva measures 3.8 mm. long and is no longer doubly flexed, but the abdomen is held out nearly straight with a slight dorsal hump (Fig. 1*b*). The colouring is much the same as in the last larva, but the orange extends on to most of the abdominal somites, the telson and uropods still being colourless. There is a short unarmed rostrum and an antennal spine, the other spines having disappeared. The antennule does not differ much from the last larva and there is still an antennal scale, although it is somewhat shorter, the breadth being greater compared with the length. The flagellum is about twice as long as the scale. The abdomen is similar in shape to that of the adult, the ends of somites 4 and 5 ending in rounded points. The sixth somite is very much shorter than in the last larva and bears two broad spines, each side posteriorly very much as in the adult. The telson is straighter and narrower than in the adult, but is similarly armed with two pairs of lateral spines and three pairs of stout spines at the end with a minute central tooth. There is also a pair of hairs in the post-larva and more in the adult between the spines. The outer angle of the uropodal exopod in the adult has a main spine and seven small spines outside it; these latter are represented in the post-larva by two spines outside the main one. Except for the continued presence of the antennal scale the post-larva agrees very well with the adult. The mouthparts were not examined. There are remains of exopods on legs 1-4, and the first and second legs are much the same as in the last larva, the second legs being about equal and not as in the adult of unequal length. Legs 3-5 end in short dactyls as in the adult. The second legs are held straight in front of the body in life and the antennules and antennae stick up in front with the flagella doubled back. It appears to be likely that the post-larva swims about before entering the sponge and perhaps undergoes several moults before entering a sedentary life. No young stages have so far been found in the sponge.

***Typton tortugae* Smith (Fig. 4)**

The post-larva was found in one of Dr Moore's Bermuda hauls in 1940. It is only 2.9 mm. in length, and there is no antennal scale, thus differing conspicuously from *T. spongicola*. The legs agree very well with Schmitt's figure and there seems to be no doubt that it belongs to this species. There are remains of exopods on legs 1 and 2 only, and not on legs 3-5. Gurney and Lebour (1941) have described a larva (*Mesocaris* A) from Bermuda which they suggest might belong to *T. tortugae*. This has exopods on legs 1-4, which seem to exclude it from this species whose larva is thus still to be found.

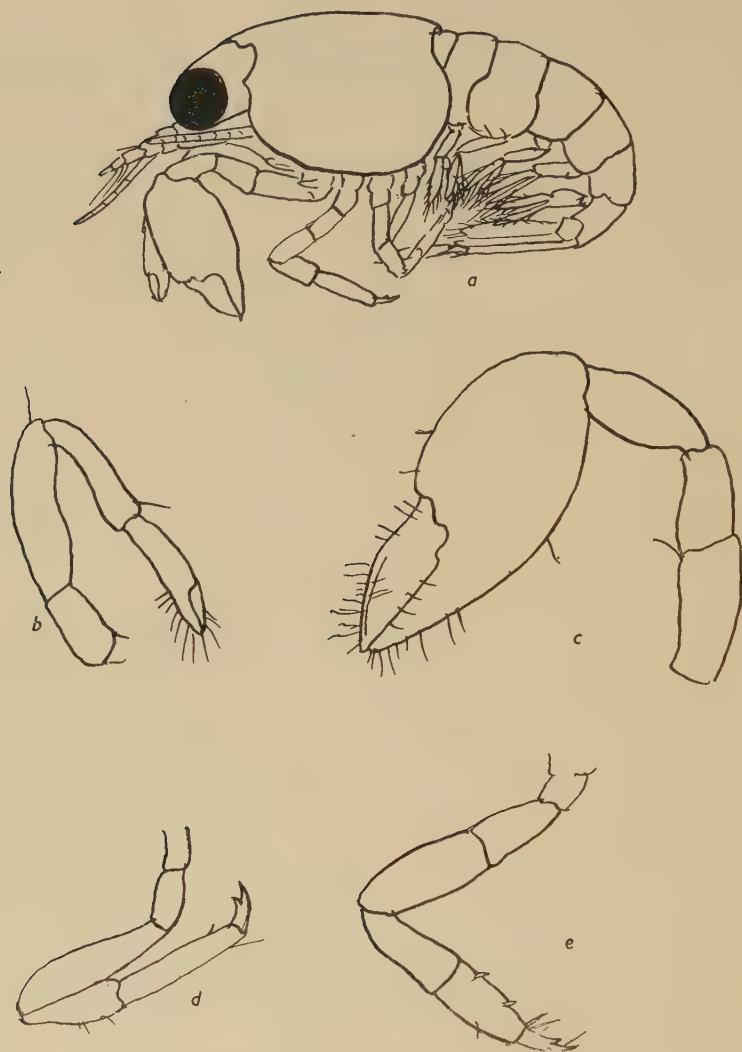


Fig. 4. *Typton tortugae*, post-larva: a, side view; b-e, legs 1-4.

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CORRELATION OF SOME OF THE PHYSICAL AND CHEMICAL PROPERTIES OF THE SEA WITH THE CHEMICAL CONSTITUTION OF THE ALGAE

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(Text-figs. 1-14)

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PART I. THE SEASONAL VARIATION IN TEMPERATURE, pH, SALINITY, DISSOLVED OXYGEN, PHOSPHATE, AND NI- TRATE IN THE INSHORE WATERS AT THREE POSITIONS ON THE ARGYLLSHIRE COAST

INTRODUCTION

Although reliable data are available for the seasonal variation of the nutrient salts of surface off-shore waters in various parts of the world (Harvey, 1945, pp. 75-8, 85-6), information on inshore coastal waters is scanty. In North

America, however, extensive investigations have been carried out within the last 20 years on the coastal waters bordering on the states of Washington and British Columbia. These waters are cut off from the Pacific Ocean by Vancouver Island, and thereby possess certain characteristic properties. Hutchinson, Lucas & McPhail (1929) have described the seasonal variations in the waters of the Strait of Georgia. The phosphate figures are much higher than in the open sea, and these authors attribute the high nutrient content to the inflow of water from the Fraser River.

The waters of Puget Sound are also particularly rich in phosphates, nitrates and silicates. Thompson & Robinson (1933) believe this to be due to upwelling off the entrance to Juan de Fuca Strait and to vigorous mixing and agitation of the waters. Phifer & Thompson (1937) give the results of 5 years' study of the inshore conditions at Friday Harbour, on the San Juan Channel. In general, the nitrate and phosphate figures are about four times higher than those reported in our waters, and they are not subject to the same marked seasonal variation, while dissolved oxygen saturations rarely exceed 80%. In this channel strong tidal currents throughout the year create turbulent conditions, which are responsible for the high nutrient and low oxygen contents of these waters.

Newcombe, Horne & Shepherd (1939) have studied the waters of Chesapeake Bay, in the region of Solomons Island, Maryland, U.S.A., during the period 1936-38. Conditions in Chesapeake Bay, however, are typically 'estuarine', surface chlorinities being low (5.8-10.2‰) and summer temperatures high (25°C.). The phosphate content of the Bay waters in summer commonly ranges about 0.23×10^{-3} mg. atom P/l. at the surface, while the river waters may contain 1.0×10^{-3} mg. atom P/l. Minimum concentrations are obtained during the winter period, when the abundance of phytoplankton organisms is maximum. Estuarine waters are rich in ammonium and silicate.

Marshall & Orr (1927) obtained a close relation between the growth of diatoms and chemical changes in the Clyde Sea Area in 1924, 1925 and 1926 and again in 1927 and 1928 (1930). In 1926 the seasonal variation in temperature, density, pH, salinity, dissolved oxygen and phosphate were determined for two points in Loch Striven. The two localities visited were Clapochlar (depth *c.* 60 m.) and Loch Striven head (depth *c.* 28 m.), and samples were taken at 0, 10, 20, 40 and 60 m. at weekly intervals from the end of January till the end of November. Loch Striven is not polluted to any extent by the Clyde, although the surface water is often affected by drainage from the hills, which give rise to erratic salinity values.

No other work, at least to the writers' knowledge, appears to have been carried out on the seasonal variation in the nutrient content of the Scottish inshore waters, and it seemed possible that lack of nutrients during the summer months might influence the growth of algae.

This investigation was undertaken, therefore, in order to determine the

seasonal variation in the nutrient content of our sea water and to ascertain if any correlation existed between the composition of the sea water, in particular, nitrate, and that of the algae growing in it.

LOCATION AND METHODS OF SAMPLING

The three positions selected were Eilean Coltair (at the entrance to Loch Melfort), Rudh-an-Aoil (Shuna Island) and Cullipool (Luing Island). Eilean Coltair is the most sheltered of the three positions, being situated in a loch with the water cut off to a certain extent. Shuna Island is more exposed, with strong tidal currents running, but it is protected from the open sea by the Island of Luing. Cullipool, situated on the north-west coast of Luing Island, is open to the Atlantic and is the most exposed position.

The upper waters pass in general direction from the Irish Sea, through the North Channel and up the west coast of Scotland, through the Minch and round the north coast to the Orkney region. The water at the three positions selected can therefore be regarded as typical coastal inshore water, practically free from oceanic water.

Samples from the three localities were taken monthly for 13 months from March 1948 to March 1949 by means of a Nansen-Pettersson water bottle at a depth of 4-5 m. (low water), just above the weed bed. Temperatures were recorded with a reversing thermometer and the transparency of the waters measured with a standard Secchi disk.

The samples of water, carefully protected from light, were transported to Inveresk Gate and the chemical analysis carried out within 24 hr.

EXPERIMENTS AND RESULTS

The usual methods for the various determinations were utilized, and the results are summarized in Tables I and II and Figs. 1-6.

The pH was measured with the Marconi pH meter, and the observed readings corrected for the rise in temperature since sampling. The pH values for the three localities are given in Table I but, because of the relative constancy for any given month during the period, only the Shuna Island figures are reproduced in Fig. 5. Dissolved oxygen was estimated only in the Shuna Island waters and the results are given in Table II and Fig. 3.

Nitrate was determined by the diphenylbenzidine method of Atkins (1932), which was modified slightly, as outlined below, to allow the colour intensities to be measured by the Spekker Photoelectric Absorptiometer. The intensity of the blue colour which develops does not bear a linear relationship to the nitrate content, but the graph of colour intensity plotted against nitrate concentration gives a smooth curve. The slope of this curve increases with increased nitrate content, so that the higher nitrate figures are more accurate than the lower figures. The accuracy of the method, however, increases from

TABLE I. SEASONAL VARIATION IN TEMPERATURE, pH AND TRANSPARENCY

Month	Temperature (°C.)			pH <i>in situ</i>			Secchi disk (m.)		
	Eilean Coltair	Shuna Island	Culli-pool	Eilean Coltair	Shuna Island	Culli-pool	Eilean Coltair	Shuna Island	Culli-pool
1948									
March	7.5	7.5	—	8.03	7.96	—	—	—	—
April	8.2	8.1	7.8	8.09	8.11	8.11	9	9	5
May	9.8	9.8	9.0	8.17	8.13	8.10	7	7	9
June	12.4	11.1	10.6	8.13	8.13	8.10	7	8	9
July	12.2	12.3	11.7	8.11	8.12	8.11	9	7	5
August	13.0	13.0	12.7	7.91	7.95	7.96	9	9	7
September	12.5	11.9	12.2	7.86	7.91	7.90	7	9	7
October	12.2	11.9	12.1	8.01	8.06	8.06	7	6	5
November	10.5	10.9	11.0	8.01	8.04	8.06	5	7	7
December	9.7	10.0	10.2	7.96	8.02	8.05	8	7	7
1949									
January	6.5	7.0	8.1	8.04	8.07	8.07	7	7	7
February	7.8	7.7	8.0	8.01	8.03	8.05	7	7	5
March	6.1	6.9	6.9	8.04	8.05	8.07	7	7	7

TABLE II. SEASONAL VARIATION IN SALINITY, OXYGEN, PHOSPHATE AND NITRATE

Month	Salinity (g./kg.)			Oxygen, Shuna Island		Phosphate (mg. atoms P/m. ³)			Nitrate (mg. atoms N/m. ³)		
	Eilean Coltair	Shuna Island	Culli-pool	ml./l. at N.T.P.	% saturation	Eilean Coltair	Shuna Island	Culli-pool	Eilean Coltair	Shuna Island	Culli-pool
1948											
March	34.05	34.12	—	—	—	0.55	0.55	—	6.4	6.1	—
April	33.56	33.81	33.94	6.24	93.5	0.35	0.52	0.41	0.7	3.1	5.0
May	33.78	33.86	34.02	6.14	95.4	0.19	0.26	0.33	1.0	2.6	4.6
June	33.90	33.93	33.93	5.94	94.9	0.16	0.20	0.18	1.4	2.4	1.6
July	33.83	33.72	33.92	6.02	98.2	0.16	0.16	0.20	0	0	0.9
August	34.01	34.02	34.05	5.73	94.9	0.19	0.19	0.20	0.5	1.0	1.5
September	33.61	33.06	33.76	5.83	93.9	0.30	0.23	0.30	3.0	3.1	4.9
October	33.63	33.57	33.65	5.71	92.4	0.37	0.31	0.31	5.0	5.4	4.8
November	33.34	33.67	33.83	5.86	93.0	0.40	0.50	0.42	4.9	5.6	5.7
December	33.16	33.59	33.83	5.85	90.4	0.75	0.65	0.50	5.5	6.1	5.7
1949											
January	32.92	32.26	33.44	6.41	92.8	0.57	0.53	0.53	6.3	6.5	6.9
February	33.45	33.62	33.56	6.40	94.3	0.51	0.53	0.53	6.5	6.7	6.5
March	33.62	33.83	34.03	7.00	101.5	0.48	0.53	0.52	5.5	5.8	5.9

± 10 mg. at 0–30 mg. nitrate—N/m.³ to ± 4 mg. at 90 mg. N/m.³. This method cannot compete with Harvey's strychnidine method at low nitrate concentrations, for the latter gives a linear relation between colour intensity and nitrate content. It was not used, however, in these investigations, because of the difficulty of preparing a satisfactory reagent.

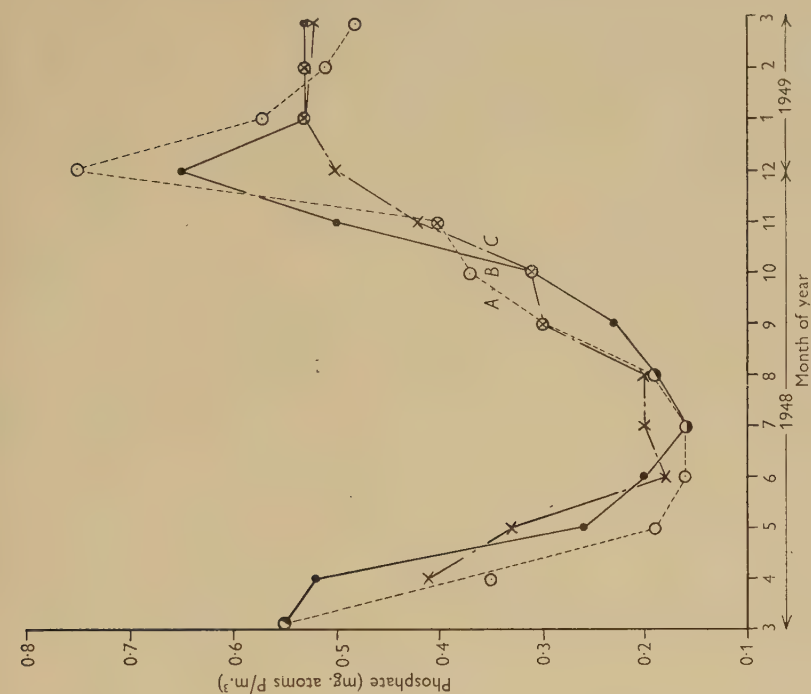


Fig. 1. Seasonal variation in temperature. (A) L. Melfort; (B) Shuna Island; (C) Cullipool.

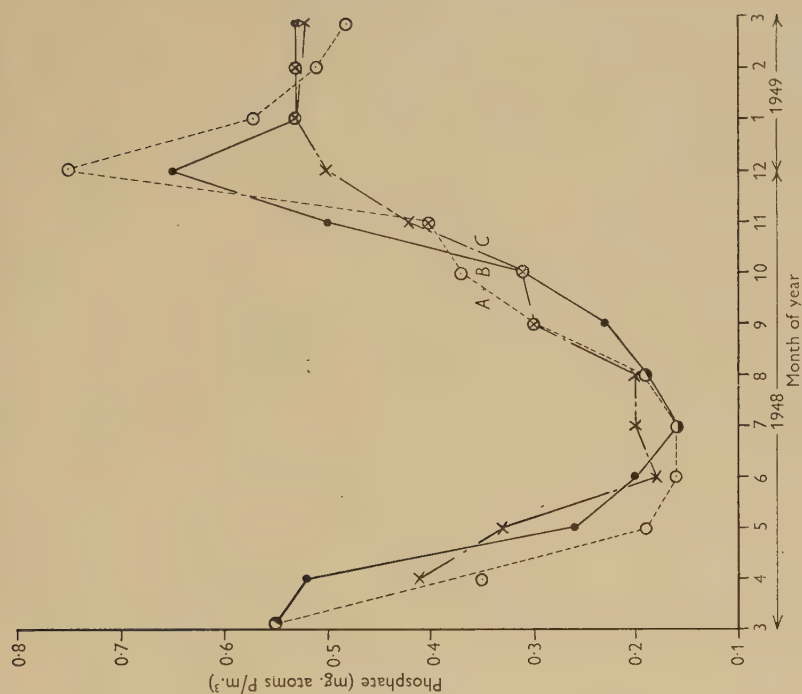


Fig. 2. Seasonal variation in phosphate. (A) L. Melfort; (B) Shuna Island; (C) Cullipool.

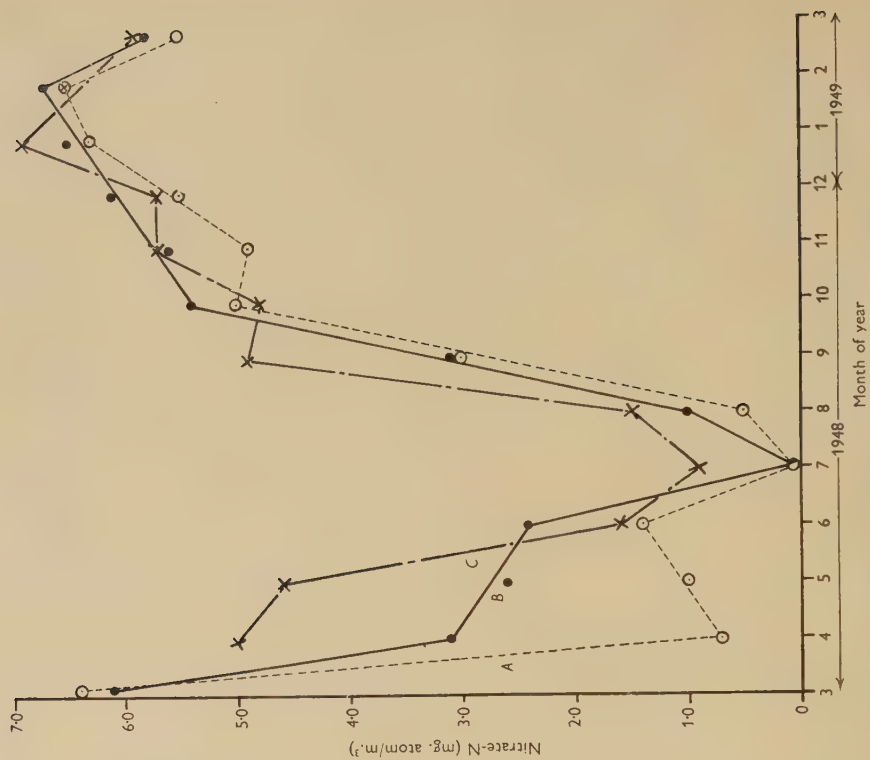


Fig. 4. Seasonal variation in nitrate. (A) L. Melfort; (B) Shuna Island; (C) Cullipool.

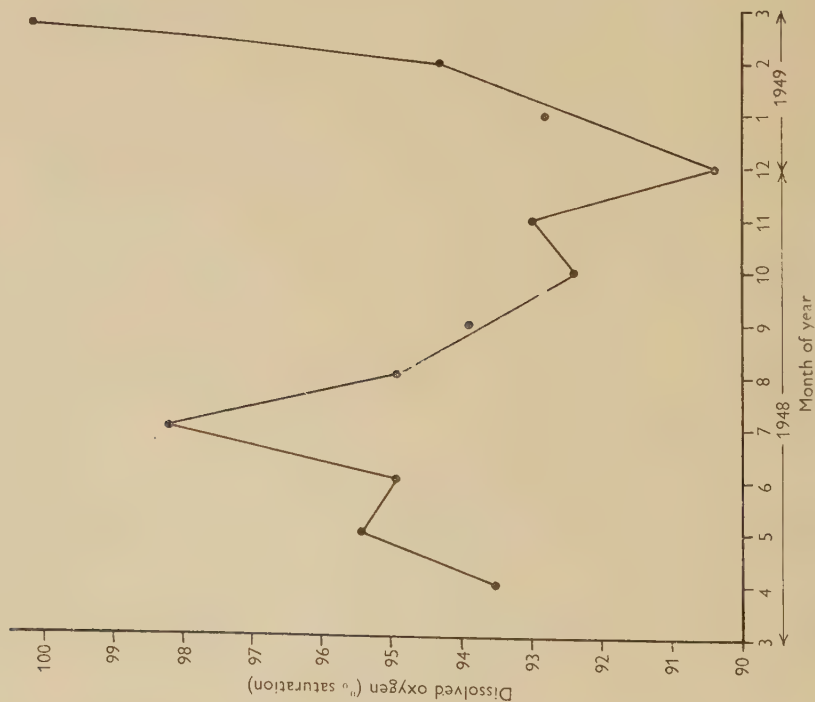


Fig. 3. Seasonal variation in dissolved oxygen. Shuna Island.

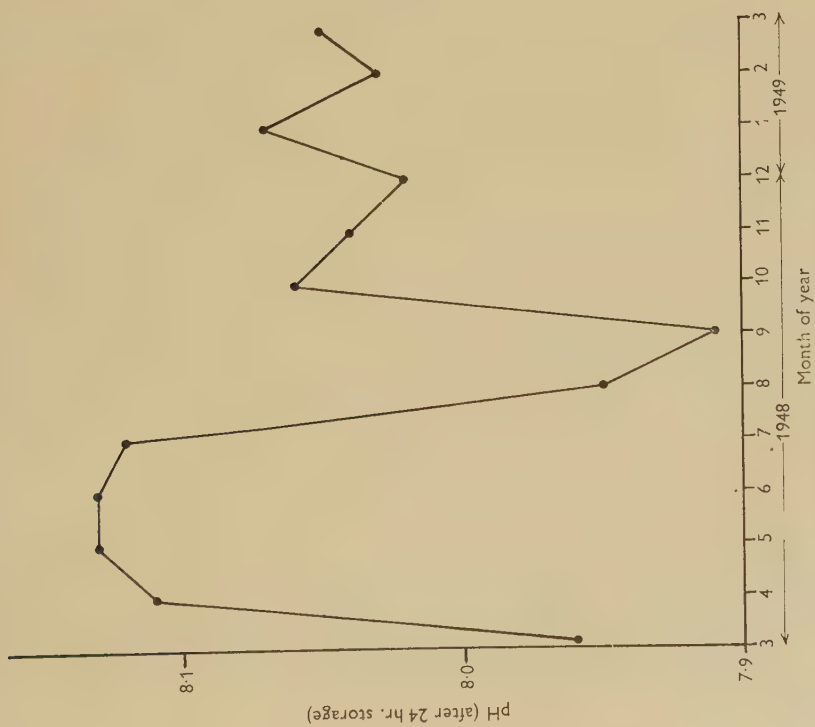


Fig. 5. Seasonal variation in pH. Shuna Island.

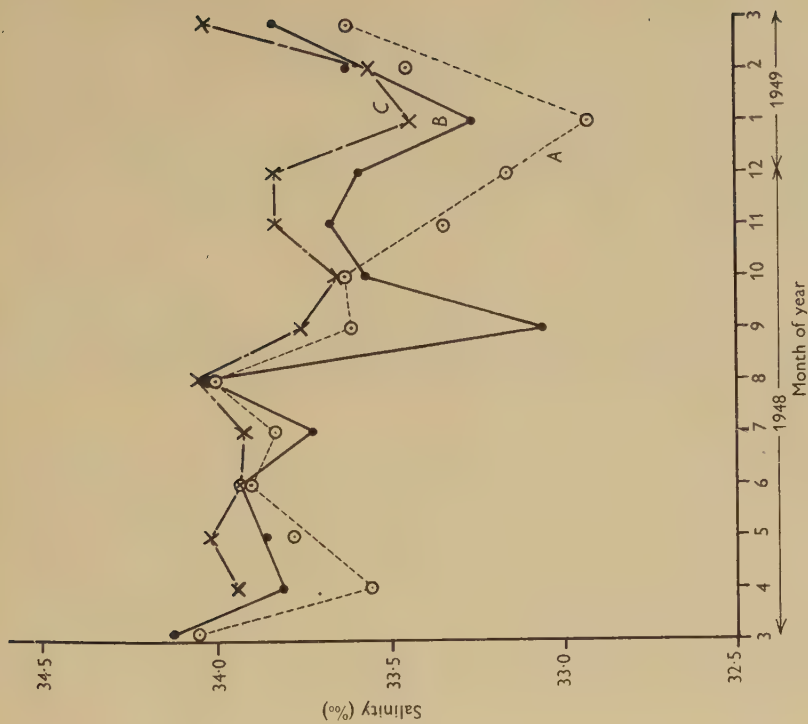


Fig. 6. Seasonal variation in salinity. (A) L. Melfort; (B) Shuna Island; (C) Cullipool.

Estimation of Nitrate

REAGENTS

Sulphuric Acid. 1 l. of H_2SO_4 (J. F. MacFarlan and Co's special nitrate free acid) was freed from traces of nitrate by heating at 300° for 2 hr. with $(\text{NH}_4)_2\text{CO}_3$ (3 g.).

Diphenylbenzidine Reagent. The diphenylbenzidine was recrystallized from boiling toluene. 20.0 mg. were dissolved in 100 ml. H_2SO_4 , the solution thoroughly shaken and allowed to stand several days before use. The final reagent was faintly blue.

Standard Nitrate Solutions. *Stock Solution A:* 0.7218 g. A.R. KNO_3 , made up to 1 l. with distilled water, gives a solution containing 0.1 g. N/litre. *Solution B:* 10 ml. solution *A* were diluted to 1 l. with distilled water or nitrate-free sea water, as required, to give a solution containing 1 mg. N/l, i.e. 1000 mg. N/m.³. *Standards C:* These were prepared from solution *B* by suitable dilution with distilled water or nitrate-free sea water as required. Solution *B* and all standards must be freshly prepared each day during calibration of the reagent.

Nitrate-free Sea Water. The sea water collected from Eilean Coltair on 11 May 1948 gave a blank not significantly greater than that given by distilled water.

CALIBRATION OF THE REAGENT

(1) *In Distilled Water*

The following standards were prepared: 100, 95, 90, 80, 75, 70, 60, 55, 50, 45, 40, 35, 25, 10 and 0 mg. N/m.³.

2.5 ml. standard in a stoppered weighing bottle were treated with 6.0 ml. H_2SO_4 , mixed and immediately cooled. The H_2SO_4 was added by means of a graduated pipette, allowing exactly 1 min. for delivery in each case. A stoppered weighing bottle was used to prevent the solution taking up water from the atmosphere on standing. After cooling, 1.5 ml. diphenylbenzidine reagent were added, the solution thoroughly mixed, and allowed to stand for 22.5 hr. in the dark. During the development period, the solutions were again mixed after 6 and 22 hr.

The blue colours developed were compared in the Spekker Photoelectric Absorptiometer, using the 1 cm. cell and the orange Ilford 607 filter. For convenience, the water setting was taken as 0.70 on the drum scale, and the drum readings found ($\log I$) subtracted from 0.70 ($\log I_0$). The values of $\log I_0/I$ for the various standards are shown in Table III.

TABLE III

Distilled water		Distilled water		Sea water		50% (v/v) sea water	
Standard	$\log I_0/I$	Standard	$\log I_0/I$	Standard	$\log I_0/I$	Standard	$\log I_0/I$
100	0.523	50	0.203	100	0.331	100	0.468
95	0.485	45	0.177	75	0.211	75	0.295
90	0.456	40	0.162	50	0.136	50	0.161
80	0.413	35	0.141	25	0.080	25	0.088
75	0.329	25	0.080	10	0.050	10	0.048
70	0.324	10	0.042	0	0.035	0	0.032
60	0.238	0	0.030				
55	0.239						

There is not a linear relationship between colour intensity ($\log I_0/I$) and nitrate concentration, but the graph gives a smooth curve.

(2) In Sea Water

In order to determine the salt error, a calibration curve was carried out using nitrate-free sea water in the preparation of the standards. The results, shown in Table III, indicate that the salts in sea water decrease the colour formation, when the colour is measured after 22.5 hr.

(3) In 50% (v/v) Sea Water

Solution *B* was made up in distilled water. The standards were prepared by taking the appropriate amount of *B*, adding 50 ml. nitrate-free sea water and making up to 100 ml. with distilled water. The results in Table III show that the colour intensities lie, for the most part, between the distilled water and sea-water values.

ESTIMATION OF NITRATE IN SEA-WATER SAMPLES

2.5 ml. of the unknown sample were treated with H_2SO_4 and diphenylbenzidine exactly as described in the calibration of the reagent, and the value of $\log I_0/I$ determined after 22.5 hr. The nitrate content of the sample in mg. nitrate-N/m.³ was read off from the sea-water calibration curve.

ACCURACY OF THE METHOD

It was found that the value of $\log I_0/I$ for any given standard could, in general, be reproduced within ± 0.02 . From the sea-water calibration curve, the accuracy at various concentrations has been estimated as follows:

Nitrate concentration	Maximum error
30 mg. N/m. ³	± 10 mg. N/m. ³
40	± 8.5
50	± 7.5
60	± 7.0
70	± 5.5
80	± 4.5
90	± 4.0

Estimation of Phosphate

Phosphate was estimated by the Denigés method, as described by Wattenberg (1937).

DISCUSSION OF RESULTS

Temperature

In the spring, temperatures are at a minimum, 6–7°C. (Table I and Fig. 1). The loch water at Eilean Coltaire gets warmer more rapidly than the open sea, reaching a temperature of over 12°C. by June. At Cullipool the surface waters take considerably longer to heat up, 12°C. only being reached in August. For Shuna Island, in general, the graph lies between the other two.

The opposite state of affairs prevails during the autumn and winter months. Cullipool maintains a temperature of 8°C. or more until February, while the loch water has dropped to 6.5°C. by January. One would expect loch water, because of its proximity to, and isolation by, land, to warm up and cool down more rapidly than the open sea. It is interesting to note that the maximum and minimum temperatures for the three positions do not vary appreciably, although the times required to reach these values do.

Marshall & Orr (1927) found the temperature of the surface waters (0–10 m.) at Clapochlar to be at a minimum (6°C.) in January/February, rising to a maximum of 14°C. in August.

pH

The pH was measured 24 hr. after sampling. The effect of storage is to lower the pH for the following reasons: (1) On standing, the water warms up to that of its surroundings, and the pH falls with rising temperature. The pH *in situ*, however, can be calculated from the pH at temperature of observation by allowing for the temperature coefficient of sea water. In most cases, the decrease in pH per 1°C. rise can be taken as 0.01 pH unit. (2) Bacteria liberate carbon dioxide in respiration, and this lowers the pH. This effect cannot be corrected for, and may be appreciable during warm weather. Although care was taken to keep the temperature of the samples as low as possible during transport, the results may be slightly low.

In April a rapid increase in pH occurs, indicating that plant growth is beginning to utilize carbon dioxide at a greater rate. From April to July the pH values for all positions are 8.10 or greater, but in August and September figures of 7.86–7.96 indicate a slowing up in the rate of photosynthesis which coincides with a low nutrient content of the water. An increase in pH occurs in October, and from October to March fairly constant values of 8.00 ± 0.07 are obtained.

The pH of the surface water at Clapochlar (Marshall & Orr, 1927) was close to 8.0 during the early part of the year. This was followed by a sudden increase at the beginning of April following the spring diatom outburst, and figures of 8.3–8.4 are recorded during this period. Another peak in the pH graph was obtained in September due to the autumn phytoplankton growth.

Transparency

It was hoped, by means of a Secchi disk, to detect the phytoplankton outburst in the spring, but in practice very little variation was observed throughout the year. Maxima of 7–9 m. and minima of 5–6 m. are recorded, but these do not occur at any specific time and appear to have no significance.

Salinity

In ocean water away from the influence of land, variations in surface salinity are not great. Böhnecke (1938) has shown for an area of the North Atlantic Ocean, extending between latitudes 18° and 42° N., that the highest average surface salinity, 36.70‰, occurs in March and the lowest, 36.59‰, in November. The variations from one month to another are irregular, but on the whole the salinity is somewhat higher in spring than it is in autumn. In the open ocean variations in surface salinity depend mainly upon variations in the difference between evaporation and precipitation, in association also with currents. In inshore waters salinity values are complicated by the influence of land, which gives rise to coastal currents and dilution due to rivers and land drainage. For example, when heavy rain falls during the winter the increased volume of waters discharged by the rivers of the region will tend to decrease the salinities during the winter months. If, however, the precipitation is in the form of snow, the effect upon the salinity of the coastal waters may not be experienced until the summer.

The high salinity values obtained in this investigation, particularly for Cullipool, indicate that these waters have not been diluted by fresh water to any great extent, and the figures bear some relation to the rainfall for the 13 months. For all positions, highest values were obtained in March and August, and lowest values in January. In September an abnormally low figure, 33.06‰, was reported for Shuna Island. In general, the salinity of Cullipool water is higher than the loch water, and this is to be expected because land drainage after heavy rain will affect loch more than open sea water. Again, the graph for Shuna Island lies between the other two for most months of the year, although there are some exceptions.

Marshall & Orr (1927) found the salinity of the surface layer at Clapochlar lay between 33 and 34‰, although some values for the immediate surface layer were much lower, for example, some very low figures are recorded during March and October/November.

Oxygen

With the exception of March 1949, the samples were treated with the reagents, manganous chloride and sodium hydroxide-potassium iodide, about 24 hr. after sampling. In March 1949, the reagents were added immediately after sampling, and the iodine liberated and titrated the following day. This water was found to be slightly supersaturated (% saturation, 101.5). Thus it may be

assumed that all the results, except the last, are low to the extent of 5–10%. Nevertheless, the relative values are of interest in detecting the period of photosynthesis in the spring. The explanation for these low results is twofold: (1) on standing, the water warms up to that of its surroundings, and a certain amount of oxygen tends to be expelled from solution at the higher temperature; and (2) when sea water is stored, bacteria rapidly consume oxygen in respiration, the amount utilized being quite appreciable even after 24 hr. Moreover, bacteria are particularly abundant in inshore water.

The highest saturations are obtained during the spring and summer months, the maximum (98.2%) being reached in July, which is further evidence of photosynthesis during these months. Saturations then decrease steadily to a minimum of 90.4% in December. Because of the uncertainty of these results, further discussion would be unwise, but it appears that this water is saturated, or very nearly saturated, for the greater part of the year, and probably slightly supersaturated during the period of photosynthesis.

Marshall & Orr (1927) found the dissolved oxygen saturations for the surface layers were close to 100% throughout the year, except during the diatom outbursts in the spring and autumn when values up to 138% were occasionally recorded.

Phosphate

The phosphate estimations were carried out one day after sampling, the water being centrifuged before analysis if any turbidity was noticed. It is advisable, however, to estimate phosphate immediately after sampling, or to saturate the water with chloroform if estimations are to be carried out at a later date. On standing, the inorganic phosphate may increase slightly if much organic phosphorus is present, or it may decrease due to utilization by bacteria, but this error will not be great after only 24 hr., provided the temperature of the water is prevented from rising appreciably.

Fig. 2 indicates that the phosphate content begins to decrease after March, the decrease being most marked in the loch water, although the open sea at Cullipool has a phosphate content in April not much greater than the loch. Minimum values of 0.16–0.20 mg. atom phosphate-P/m.³ are obtained in all localities by June, and remain at this low level until September, when there is an increase again to the winter maximum in December, January and February. Abnormally high values were obtained in December for Eilean Coltair (0.75 mg. atom P/m.³) and Shuna Island (0.65 mg. atom P/m.³), which can only be attributed to contamination by land drainage, as the value for Cullipool was normal.

The winter maximum for 1949 of 0.52 mg. atom P/m.³ is in good agreement with the values quoted for the English Channel, although the summer minimum tends to be higher than that found in the Channel.

The seasonal variation in phosphate at a position in the English Channel

has been followed at monthly intervals for a number of years. From winter maximum values varying between 0.69 and 0.47 mg. atom P/m.³ it has fallen in some years to less than 0.02 in the surface layers, in other years 0.06 or 0.10 mg. atom remain (Atkins, 1923-30; Cooper, 1933 *a, b*, 1938). The winter maximum values of phosphate in the water at the beginning of the year are not constant but fluctuate from year to year. Cooper (1938) has found lower winter maxima during the 1930's as compared with the 1920's, and these have been reflected in decreased plankton and fish populations (Russell, 1935, 1936 *a, b*).

During February at Clapochlar (Marshall & Orr, 1927), phosphate in the surface layer was about 0.65 mg. atom P/m.³. Within a few weeks, at the end of March and beginning of April, phosphate was reduced to 0.16 mg. atom P/m.³, while by the end of May no trace of phosphate existed in the surface layer. Small quantities appeared in the waters at odd periods throughout the summer, but no full-scale regeneration of phosphate became apparent until the end of September. Maximum winter values were obtained by November.

Nitrate

The estimations were carried out 1 day after sampling. The effect on the nitrate content of storing samples for 24 hr. is negligible, provided the samples are shielded from light. Fig. 4 shows that the seasonal variation of nitrate follows closely that of phosphate. After March nitrate begins to decrease, and again this decrease is most marked in the loch. Between March and April 1948 nitrate-N in Loch Melfort dropped from 6.4 mg. atoms/m.³ to almost zero, and remained at this level until September. Complete exhaustion of nitrate was not observed at Shuna Island and Cullipool until July. Nitrate is almost certainly absent in all localities during July and August. As in the case of phosphate, nitrate is regenerated during September and increases gradually during the autumn and winter, reaching a maximum of about 6.8 mg. atoms N/m.³ in January. Little or no evidence was obtained of the plankton outburst in the autumn, either from the phosphate or nitrate records.

The seasonal variation in nitrate has been followed during the course of several years in the English Channel (Harvey, 1926, 1928; Cooper, 1933 *a*). Exhaustion of nitrate due to utilization by phytoplankton is frequently found in the surface water during the summer, while winter maxima may exceed 7 mg. atoms nitrate-N/m.³. The absence of nitrate, however, does not necessarily mean that plant production in the sea is reduced to a low level, as nitrogen may still be available as ammonium, the concentration of which may reach 2 mg. atoms ammonium-N/m.³ during the autumn and winter months. Harvey (1940) has shown that plankton diatoms utilize ammonium in preference to nitrate. This may explain why the autumn plankton outburst was not detected by following the seasonal variation in nitrate (Fig. 4), although the flattening of the graph from September to December might be taken as an

indication of its utilization by plankton. In the spring, nearly all the available nitrogen is present as nitrate.

The Nitrogen/Phosphorus Ratio at the Winter Maximum

If 0.52 mg. atom P/m.³ and 6.8 mg. atoms N/m.³ are taken as the winter maximum values for phosphate and nitrate respectively in 1949, the N/P ratio is 13.2.

The significance of these results on the growth of the adjacent seaweeds is discussed in Part II.

SUMMARY

Monthly samples of sea water, taken from three localities on the Argyllshire coast, from March 1948 to March 1949, have been analysed for pH, dissolved oxygen, salinity, nitrate and phosphate, while temperatures and transparencies have been recorded.

Surface temperatures range from 6–7°C. in January/March to 13° in August. Transparencies remain fairly constant at 7–9 m. throughout the whole period, with occasional minimum values of 5–6 m.

pH values close to 8.0 are obtained from October to March, followed by an increase to 8.1 or over during the period of photosynthesis (April to July). Low pH values (7.86–7.96) are recorded during August and September.

Salinities vary over the narrow range, 33–34‰, with maxima in March and August and minima in January. These high salinities indicate that the inflow of fresh water from streams in the neighbourhood is negligible, even for Loch Melfort.

Dissolved oxygen saturations are highest in the spring and summer months and lowest in December.

Phosphate and nitrate begin to decrease after March, the reduction being most marked in the loch, and remain at a low level until September, when these nutrients are again regenerated. Winter maximum values of 0.52 mg. atom P/m.³ and 6.8 mg. atoms nitrate-N/m.³ are obtained by January.

Atkins's diphenylbenzidine method has been used to estimate nitrate, and a description of the method is given.

PART II. CORRELATION OF THE COMPOSITION OF SEA WATER WITH THE CHEMICAL CONSTITUTION OF THE ALGAE

INTRODUCTION

The larger algae, like most other forms of marine plant life are, apart from the influence of light, wholly dependent for their growth and development on the nutrient content of the surrounding sea water.

Although there is no experimental evidence to show that the growth rate of sea-weeds in the sea is ever brought to a standstill through lack of nutrients, Harvey's work (1926) indicated that lack of nitrate can limit plant growth. He also showed (1933) that a marked reduction in the rate of photosynthesis for the diatom *Nitzschia closterium* occurred with phosphate concentrations below 0.32 mg. atom P/m.³, being most marked below 0.16 mg. atom P/m.³. There appears to be no doubt that nitrate and phosphate are most important factors in the productivity of the sea, and plankton, at least, is richer where vertical currents aid in increasing their concentration. Whereas Harvey (1926, 1928) has recorded marked seasonal variations in the nitrate-content in the English Channel with non-detectable amounts in August, Dakin (1934) showed that at Sydney there was a much more uniform distribution throughout the year. It would appear, therefore, that marked seasonal variations in the nutrient content, with depletion of nitrate in the summer, occur mainly in inshore waters where a thermocline is set up during the summer preventing regeneration of the nutrients in the photosynthetic layer.

Marshall & Orr (1948), in carrying out experiments in Loch Craiglin on the effect of different plant nutrients on the phytoplankton, found that after adding a large excess of fertilizer a good increase in plankton was obtained, after an initial lag. At that time attached algae were abundant and these investigators believed that the needs of the algae had to be satisfied before any nutrients could be used by phytoplankton.

With marine diatoms, therefore, scientific investigations have established a direct correlation between their efflorescence and abundance, and the concentrations of nutrient salts, especially nitrates and phosphates, in sea water, and scientific literature pertaining to European, American, Antarctic and other waters furnishes numerous examples.

Parke (1948), in her studies on the British Laminariaceae, found for *Laminaria saccharina* that there were two periods of growth, a period of rapid growth between January and June/July with the most rapid growth between March and June, and a period of slow growth from July to December, but unfortunately no attempt was made to correlate this with the nutrient content of the water.

Tikhovskaya (1940) investigated the seasonal variations in the productivity and photosynthesis of *L. saccharina* in the Barents Sea. He reported maximum

growth in April with a sharp drop in June and a slight increase in October, and stated, although no figures are given, that in summer the N and P content was the smallest for the whole year.

In view of the fact that in Norway, it has been possible to correlate the presence of herring with water of a particular temperature and salinity, it was thought that, since correlation appeared to exist between the chemical composition of the algae and the physico-chemical properties of the water, it might be possible from an analysis of the water to forecast the optimum annual harvesting periods. No previous investigator, however, appears even to have attempted to correlate the seasonal changes in the chemical composition of the fixed algae with changes in the composition of the sea water.

PREPARATION AND ANALYSIS OF SAMPLES

Monthly samples comprising six plants of the following species of Laminariaceae were taken, two were used for dry weight determinations, and two were analysed by the methods previously employed (Black, 1948).

The inorganic nitrogen was obtained by difference, i.e. by subtracting the organic nitrogen from the total nitrogen. The total nitrogen was determined by modifying the standard Kjeldahl method using a reduction mixture containing sodium thiosulphate as a preliminary, to the ordinary digestion (Kelley, Hunter & Sterges, 1946). Any ammonium salts, however, present in the plant will be estimated as organic nitrogen (Kjeldahl).

- (1) *L. saccharina* from 4 m. (low water) at Eilean Coltair, Loch Melfort.
- (2) *L. saccharina* from 4 m. at Rudh-an-Aoil, Shuna Island.
- (3) *L. cloustoni* from 4 m. at Cullipool, Luing Island.

The results for crude proteins, inorganic nitrogen, mannitol, laminarin, dry-weight content, fresh weight, total ash, and alginic acid are summarized in Figs. 7-14.

As the marked seasonal variations in composition occur in the fronds the results for the stipes, with the exception of the fresh weights for *L. saccharina*, have been omitted.

DISCUSSION OF RESULTS

In comparing the variations in chemical constitution it should be borne in mind that *L. cloustoni* differs in many respects from *L. saccharina*, and it is unfortunate that the latter species was unobtainable at Cullipool.

On the west coast of Scotland, with *L. saccharina*, growth of the new frond begins much earlier than with *L. cloustoni*, and from August losses due to the shedding of the old frond of the current year may exceed the weight increment. In the autumn the rapid drop in laminarin may be due to this or it may be due to sporogenesis. On the other hand, *L. cloustoni* does not usually cast its old frond until April/May, although considerable wear has no doubt occurred

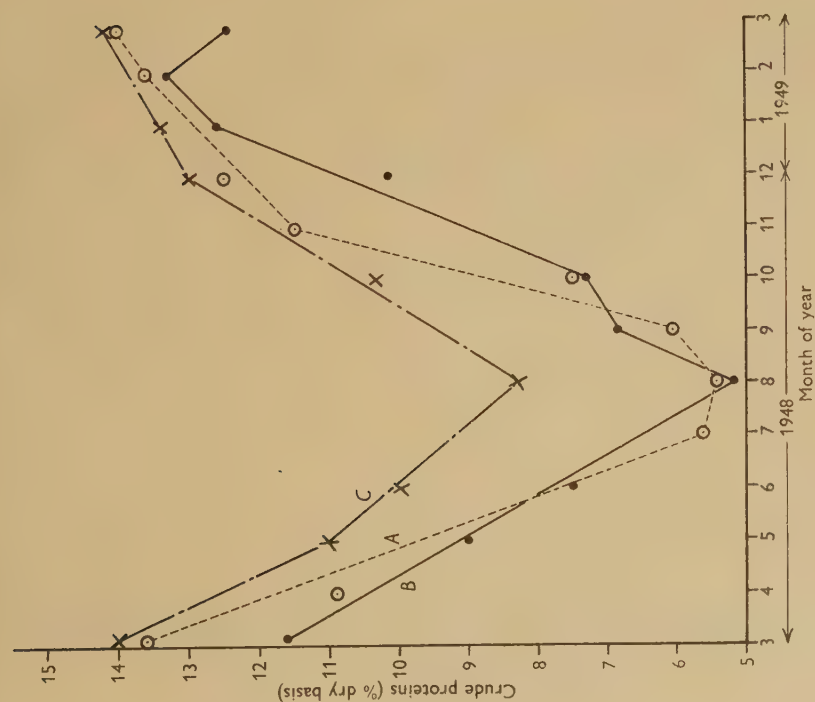


Fig. 7. Seasonal variation in crude proteins. (A) *L. saccharina* frond, L. Melfort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool.

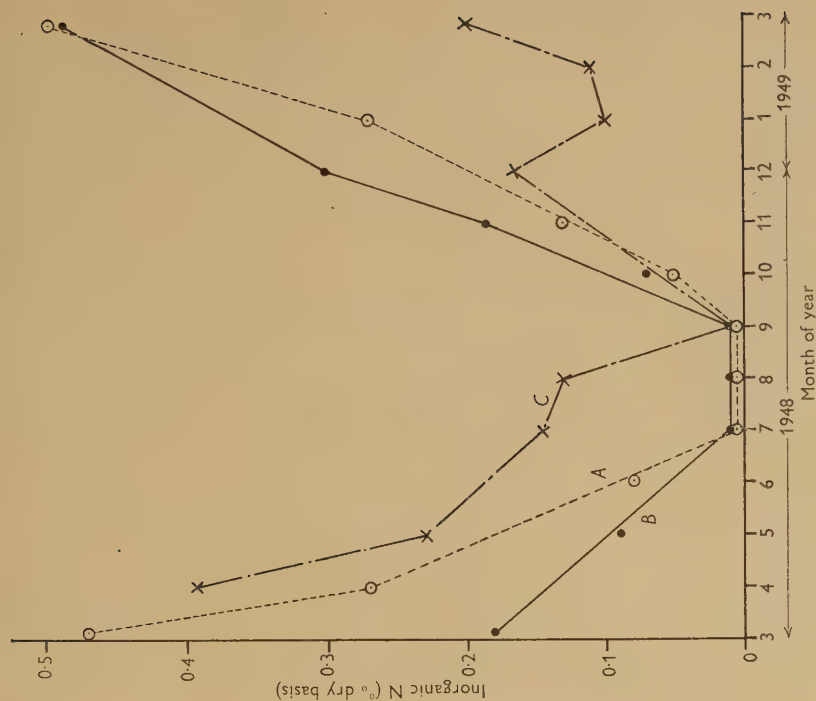


Fig. 8. Seasonal variation in inorganic nitrogen. (A) *L. saccharina* frond, L. Melfort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool.

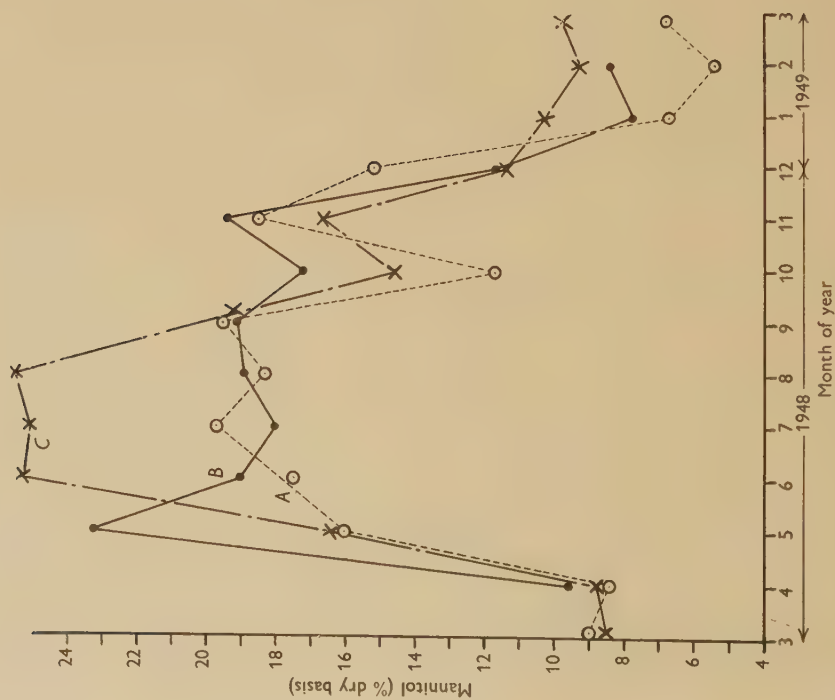


Fig. 9. Seasonal variation in mannitol. (A) *L. saccharina* frond, L. Mel-fort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool.

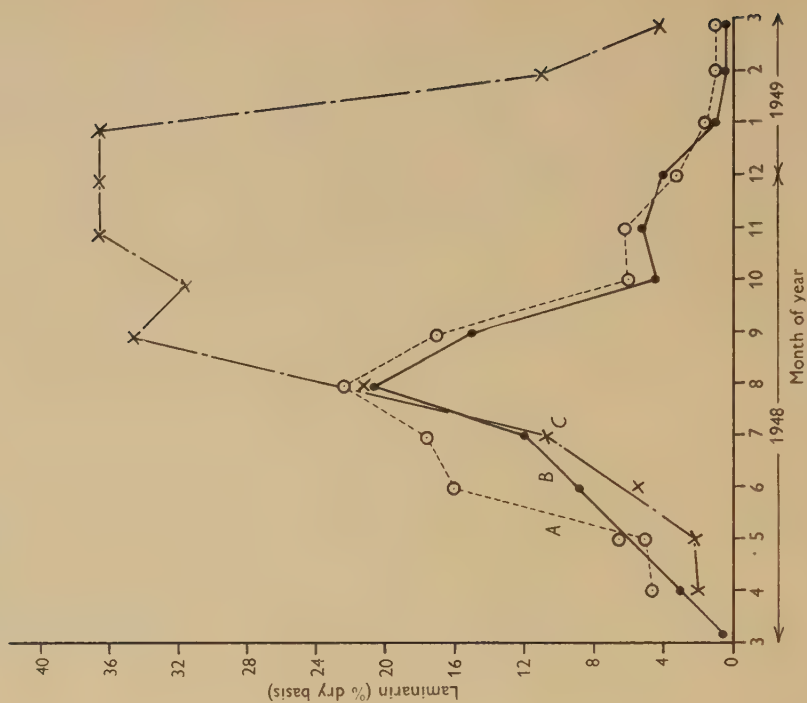


Fig. 10. Seasonal variation in laminarin. (A) *L. saccharina* frond, L. Mel-fort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool.

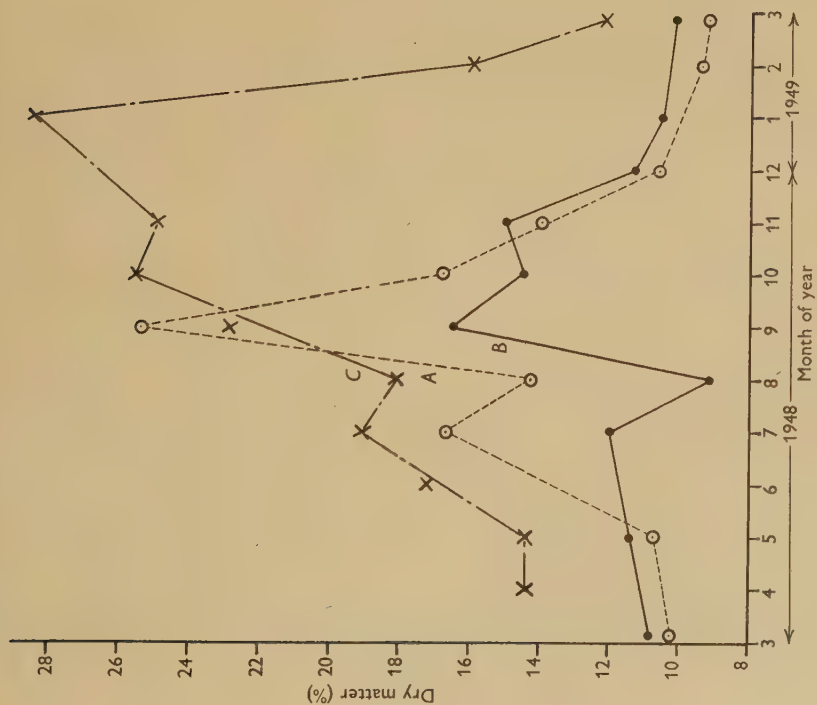


Fig. 11. Seasonal variation in dry matter. (A) *L. saccharina* frond, L. Melfort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool.

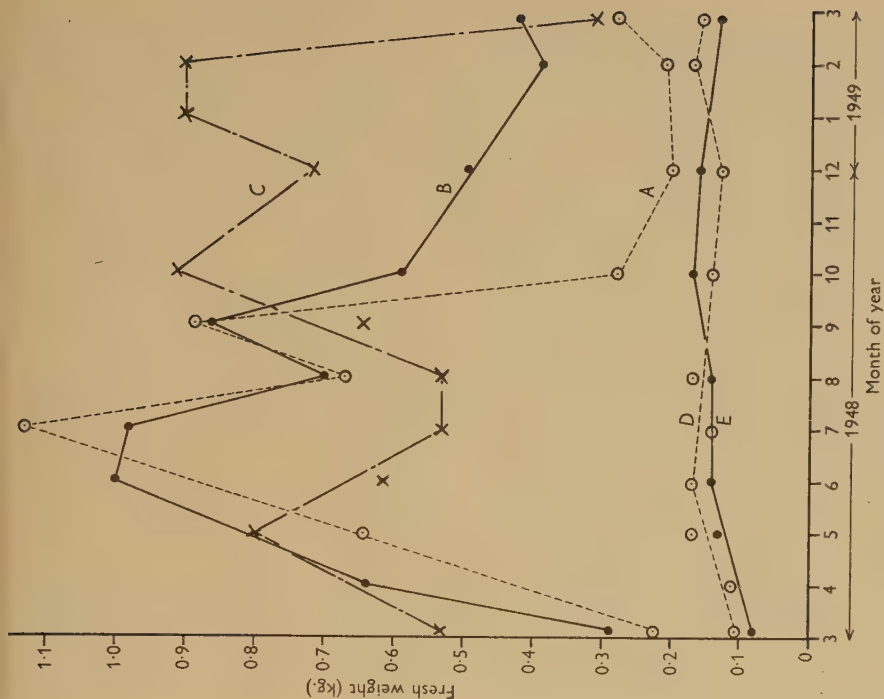


Fig. 12. Seasonal variation in fresh weight. (A) *L. saccharina* frond, L. Melfort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool; (D) *L. saccharina* stipe, L. Melfort; (E) *L. saccharina* stipe, Shuna Island.

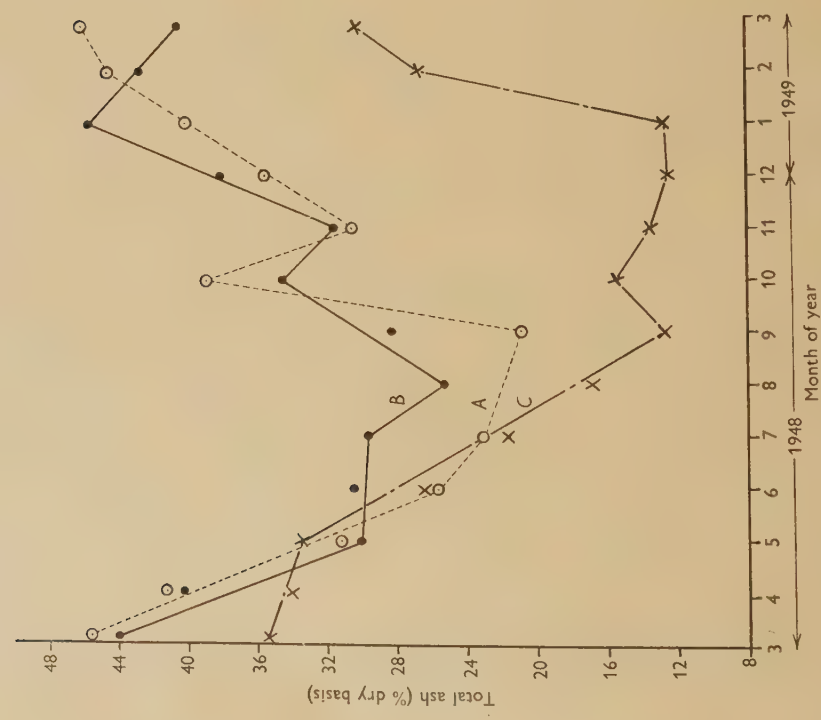


Fig. 13. Seasonal variation in total ash. (A) *L. saccharina* frond, L. Melfort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool.

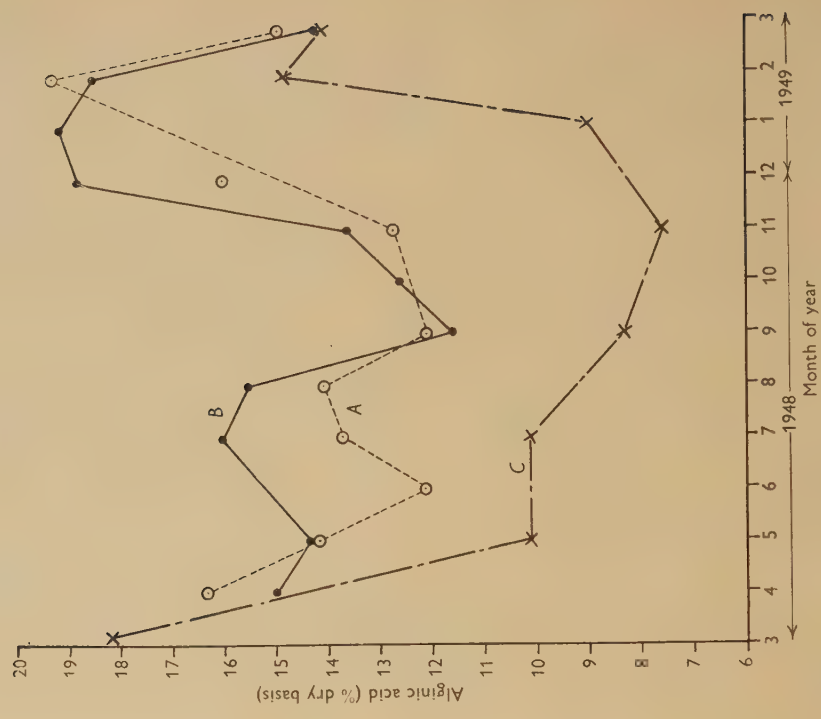


Fig. 14. Seasonal variation in alginic acid. (A) *L. saccharina* frond, L. Melfort; (B) *L. saccharina* frond, Shuna Island; (C) *L. cloustoni* frond, Cullipool.

before then. As distinct from *L. saccharina* laminarin is found at a high percentage in January when sporing of this species usually occurs. With *L. cloustoni*, therefore, the new frond may begin growth in water already depleted of nutrients, and this may account to some extent for the results obtained, and particularly the high laminarin content which the writers believe to be an indication of 'restricted growth'. It may be significant, however, that *L. saccharina* is often regarded as an annual, while *L. cloustoni* is a perennial.

In this investigation the plants have been weighed, but these weights cannot be taken as a measure of growth. First, differences may be due to variations in the weights of the individual plants; and secondly, the weight is determined by the rate of growth minus the rate of wear. Sporogenesis may also influence the weight, as a sporogenous frond has been found to be approximately twice as heavy as a sterile one (Report by State Oceanographical Institute, 1933).

It might be argued that the results expressed on the anhydrous basis do not give a true picture of the living plant and that a decrease in a particular constituent, for example, is due to growth and its redistribution in a larger plant. When the results are calculated on the wet basis, however, the graphs are, in general, parallel to those for the anhydrous basis.

The results, on the other hand, could be expressed per unit plant. If we consider the crude protein content, the maximum in the fronds, on the anhydrous basis, occurs in March 1948, when it is 50 g. per fresh frond. In August when it is at a minimum, on the anhydrous basis, it is 140 g. per fresh frond. In March the proteins will consist of reserve proteins and protoplasmic proteins. During rapid growth, however, the reserve proteins will no doubt be utilized to produce protoplasm; and synthesis of proteins, and consequently growth, will continue as long as inorganic nitrogen is present in the sea water or in the plant. By August the reserve proteins may all have been converted, and absence of inorganic nitrogen both in the water and the plant will consequently retard growth.

Although many of the changes in the composition of the sea water, such as the rapid utilization of nitrate in the spring, may in part be due to phytoplankton, during the summer, when the light is strong, plankton probably keep well below the surface and out of the sea-weed zone.

If carbohydrate assimilation with a corresponding decrease in crude proteins and ash can be taken as a measure of photosynthesis, the results indicate that a period of rapid photosynthesis occurs from March to June/July. During this period, with the exception of *L. cloustoni*, an increase in the fresh weight of the plants occurs indicating that this is also a period of rapid growth. A marked increase in the pH and oxygen saturation is further evidence of rapid photosynthesis. Growth and/or photosynthesis during this period utilizes all the nutrients in the water, so that by August nitrate is undetectable and phosphate is as low as 0.16–0.19 mg. atom/m.³. The warming of the waters may have resulted in the setting up of a thermocline, thereby restricting vertical mixing

so that regenerated nutrients do not reach the photosynthetic layer. In September cooling of the waters results in the autumn mixing and the replenishment of the photosynthetic layer with nutrients, so that in October/November a second burst of photosynthesis but on a reduced scale occurs, resulting again in increased carbohydrate assimilation. With light, no doubt, now the limiting factor, photosynthesis slows up and the nutrients accumulate again to reach their winter maxima in January/February.

In foreign waters such as the San Juan Channel, Washington, U.S.A., where *Nereocystis luetkeana* predominates, nitrate and phosphate have been determined for a period of 5 years (Phifer & Thompson, 1937). The great velocity of the tidal currents there creates very turbulent conditions and no thermocline is set up as in our inshore waters. At all times of the year the phosphate concentration was always sufficient for plant growth and could never be considered as a limiting factor. From a maximum of about 3 mg. atoms/m.³ in December it decreased to 0.8 mg. atom/m.³ in August, and this minimum value is considerably greater than our winter maximum. Nitrate, at a maximum of about 35 mg. atoms/m.³ in December/January, dropped to 0.5 mg. atom/m.³ in August, a minimum value of the order of magnitude of our winter maximum.

Although it appears that some correlation exists between the seasonal variation in the composition of the British Laminariaceae and variations in the sea water, it does not appear evident to the authors how, by taking and analysing a sample of sea water, it is possible to predict the appropriate time of harvesting, when a desired constituent will be at a maximum. A 4-year investigation (Black, 1948, and in the press) of the seasonal variation of some of the common British Laminariaceae has provided that information. To establish the correlations between the physico-chemical properties of the water and the fixed algae would require quite extensive work over a period of years, and once established it would still be necessary to keep sampling the sea water at intervals to ensure that the prognostication was being followed as expected.

In March the fronds of the *Laminaria* are low in mannitol and laminarin (Figs. 9 and 10) and high in proteins and inorganic nitrogen (Figs. 7 and 8), after the carbohydrates have been used up during the winter in respiration and probably in the synthesis of proteins, which are believed to be the product of a 'dark' synthesis. In March also, the alginic acid content is at a maximum (Fig. 14), but the frond is exceedingly small (Fig. 12) and high in water content (Fig. 11), while the cell sap contains much mineral matter (Fig. 13). During the winter months the rate of photosynthesis has been very low, if any photosynthesis occurs at all, and consequently the surrounding sea water is high in nitrates and phosphates.

In March/April a marked increase in photosynthesis occurs, accompanied by an increase in the fresh weight of the plant and an increase in the mannitol, while a decrease occurs in the crude proteins and inorganic nitrogen, all

indicating that vigorous growth has commenced. Simultaneously, in the surrounding sea water a drop occurs in the nitrate and phosphate content as a result of their utilization by algae and other forms of marine life. At the same time an increase in the pH and oxygen saturation content occurs, which is further evidence of a marked increase in photosynthesis.

While a drop of only 0.03 mg. atom/m.³ occurs in the phosphate content of the water at Shuna Island, the phosphate content at Loch Melfort falls 0.20 mg. atom/m.³ during March/April. The change in the nitrate content is more marked during this period; at Shuna Island it falls from 6.1 to 3.1 mg. atoms/m.³, while at Loch Melfort it decreases from 6.4 to 0.7 mg. atom/m.³.

During May photosynthesis continues. *Laminaria saccharina* increases in weight, but a decrease in the weight of *L. cloustoni* occurs, no doubt due to the shedding of the old frond at this time. Mannitol shows an increase, and a decrease occurs in the crude proteins, inorganic nitrogen, alginic acid and ash. In the sea, the temperature of which is gradually increasing, the pH and oxygen saturation content show an increase, and a marked drop in the nitrate content at Cullipool and Shuna Island occurs, while phosphate decreases to 0.33, 0.26 and 0.19 mg. atom/m.³ at Cullipool, Shuna Island and Loch Melfort respectively.

In June there is a suggestion of a 'falling off' in the rate of photosynthesis. The fronds of *L. saccharina* from Shuna Island show a decrease in mannitol, but an increase in fresh weight, however, occurs in both samples of *L. saccharina*, while a decrease in the weight of *L. cloustoni* is recorded. The crude proteins, inorganic nitrogen, ash and alginic acid contents show a further decrease with an appreciably higher protein figure for *L. cloustoni* at Cullipool. While the pH and oxygen saturation of the water remain constant, a further drop in the nitrate content occurs, while phosphate is between 0.16 and 0.20 mg. atom/m.³.

In July/August there is evidence of a marked change in the rate of growth and/or the rate of photosynthesis. Laminarin shows an increase but this is characteristic of 'restricted' growth, mannitol remains relatively constant, but a drop occurs in the dry matter and fresh weight of *L. saccharina*. The water analysis shows the temperature rising to a maximum of 13°C. at the three localities. In July, nitrate and phosphate are at a minimum, the nitrate being 0.9 mg. atom/m.³ at Cullipool, while at Shuna Island and Loch Melfort it is undetectable in the water, and phosphate is between 0.16 and 0.20 mg. atom/m.³.

The pH and dissolved oxygen saturation, which reach maxima in July, fall rapidly in August, indicating reduced photosynthesis in the water. The ash content shows a slight decrease, but a marked increase occurs in the alginic acid content.

The months of July and August appear to be critical ones, and in all our work, and in the work of other investigators, comment has been passed on the change

in composition and rate of growth which occurs at this time. There may be other influencing factors, but the water analysis shows that lack of nutrients must be a limiting factor. Although low concentrations of nitrate, for example, exist in the water at Loch Melfort in April the weed still contains a reserve of inorganic nitrogen, so that it is not until July, with the exception of *L. cloustoni* which always exhibits a lag, that nitrate is undetectable in the plant and the water.

Temperature may also be an influencing factor, as it reaches a maximum of 13°C. at this time of the year. The intensity of respiration and assimilation increases with temperature, but the effect on respiration is considerably greater than on assimilation. Consequently with increasing temperature, the surplus will eventually disappear and growth will cease.

In September/October a rise occurs in the protein content of all the plants, coinciding with an increase in the nitrate and phosphate contents of the water. This is the result of the autumn cooling of the water bringing about the breakdown of the thermocline, giving vertical mixing and regeneration of nutrients in the photosynthetic zone. A marked increase in the pH of the water signifies a second 'burst' of photosynthesis, less intense however, than the spring outburst. An increase in the fresh weight and dry-matter content occurs, but a considerable drop in the laminarin occurs which might be the result of further growth.

In November/December, although a drop in the dry matter and fresh weight of the plants occurs, there is a rise in the mannitol, laminarin and crude protein contents and a decrease in the ash, indicating that the rate of assimilation still exceeds the rate of respiration. The rapid increase since August in the nitrate concentration is checked, indicating its utilization.

From December to March photosynthesis proceeds at a low rate as light may now be the limiting factor. Little change occurs in the pH, while the carbohydrates are now utilized in growth and respiration at a greater rate than they are assimilated.

Nitrate and phosphate increase to a maximum in January/February and then begin to decrease again, the exception being the high phosphate figures for Shuna Island and Loch Melfort in December.

The large store of inorganic nitrogen present in the fronds during the winter and early spring is rather surprising and is worthy of further investigation.

These seasonal variations in composition appear to be characteristic of most forms of marine life. For example, Daniel (1922) investigated the seasonal variation in chemical composition of the mussel and found from May onwards a decrease in the proteins, on the dry ash free basis, reaching a minimum in September/October and then rising to a maximum the following March. The carbohydrates showed a steady increase from March, reaching a maximum in September/October, with a tendency to form a second maximum in December, and then a rapid decrease until March.

ACKNOWLEDGEMENTS

The work described in this report forms part of the programme of research and development on seaweed undertaken by the Scottish Seaweed Research Association, to whom the authors are indebted for permission to publish. They also wish to thank the staffs at the Marine Stations at Aberdeen, Millport and Plymouth for their very valuable help, and for the loan of essential apparatus.

The assistance of Miss B. Graham and Mr W. Cornhill in the analytical work is also acknowledged.

SUMMARY

Monthly samples of the Laminariaceae, *L. saccharina* and *L. cloustoni*, from three localities on the Argyllshire coast have been taken from March 1948 to March 1949, and analysed for dry matter, ash, mannitol, laminarin, crude proteins, inorganic nitrogen and alginic acid, and the seasonal variation in these constituents correlated with the changes in composition of the sea water.

The results show that a correlation does exist and that a period of rapid photosynthesis occurs from March to June/July, but is restricted in July/August when nitrate is undetectable in the water and phosphate is as low as 0.16–0.20 mg. atom/m.³. The replenishment of the photosynthetic layer with nutrients is retarded in July/August, apparently due to the warming of the inshore waters, which may set up a thermocline restricting vertical mixing.

The autumn cooling of the uppermost waters facilitates vertical mixing, regenerating the nutrients in the photosynthetic region, and a second burst of photosynthesis at a reduced rate from the spring 'outburst' occurs in October/November.

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A SOURCE OF ERROR IN THE ABSORPTIOMETRIC DETERMINATION OF INORGANIC AND TOTAL PHOSPHORUS IN SEA WATER

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From the Plymouth Laboratory

In the course of phosphate determinations by the Denigès method it has been noticed that use of stannous chloride solutions containing some stannic tin and a low concentration of hydrochloric acid may give misleadingly high values for the reagent blank in distilled water, when the extinctions¹ of the solutions are measured with a photoelectric absorptiometer in red light (Harvey, 1948). In daylight the solutions may show a perceptible yellow colour, or even, in extreme cases, a turbidity.

The magnitude of the effect has now been measured in reagent blank determinations with distilled water and in phosphate determinations with sea water. In sea water it is smaller or non-existent, so that the reagent blank value is inappropriate and causes over-correction of the measured phosphate content of the samples, leading to fictitiously low results.

The error may be from 1 to 2 mg./m.³ of phosphate-phosphorus, or even higher when a turbidity is to be seen. It may be eliminated by ensuring that the stannous chloride solution contains about 5% by volume of concentrated hydrochloric acid.

The effect was first observed when an aged stock solution of stannous chloride was diluted with water to give a working solution which contained the required 0.3–0.45 mg. of stannous tin in three drops. When this was added to blank solutions these became faintly yellow in colour and the measured extinctions were greater than was expected. The stock solution had been prepared by dissolving 16 g. of Analar stannous chloride in 40 ml. of a solution containing equal volumes of concentrated hydrochloric acid and water. It had undergone aerial oxidation in the course of 11 months, and a test showed that only 53% of its tin content was in the stannous form. It seemed likely that the presence of stannic tin in this solution had caused the high extinction values found, by producing a colloidal suspension of basic stannic compounds which absorbed or scattered light. Since the production of these compounds is known to be hindered in presence of hydrochloric acid, the experiment of diluting this aged stock solution with 5% v/v hydrochloric acid

¹ The term 'extinction' is here used to denote the function $\log_{10} I_0/I$, where I_0 and I are the intensities of the light entering and leaving the coloured solution. In the concentrations used, the molybdenum blue colour obeys the Beer-Lambert law so that extinction is proportional to the amount of blue compound present. All measurements were made in a 15 cm. cell.

instead of water was tried. (When diluted with water only, the resulting solution contains about 0.8% by volume of concentrated hydrochloric acid.) When the more acid solution was used for reagent blank determinations the extinction measured was found to be about one-third of that given by the stock solution diluted with water, and no yellow colour was apparent.

Other concentrations of hydrochloric acid were tried with the results shown in Table I. The reagent blank solution contained 67 ml. of distilled water and 3 ml. of a reagent containing 18% by volume concentrated sulphuric acid and 10.7% ammonium molybdate. The dilute stannous chloride solutions were adjusted so that each contained 0.45 mg. stannous tin in the 3 drops used. The best concentration appears to be 5% by volume.

TABLE I. INCREASE IN EXTINCTION (MEASURED IN RED LIGHT) OF A REAGENT BLANK SOLUTION UPON ADDITION OF STANNOUS CHLORIDE

Stock stannous chloride diluted with	Increase in extinction (in 15 cm. cell)	Calculated reagent blank (mg. phosphate-P/m. ³)
Water	0.024	2.9
	0.024	2.9
1 % v/v HCl	0.020	2.4
	0.022	2.6
2 % v/v HCl	0.010	1.2
	0.009	1.1
5 % v/v HCl	0.009	1.1
	0.009	1.1
10 % v/v HCl	0.012	1.4
	0.012	1.4

To see how the reagent blank was affected by varying stannic tin content of the stannous chloride solution, three solutions were made as follows:

(1) By dissolving 16 g. of $\text{SnCl}_2 \cdot 2\text{H}_2\text{O}$ in 40 ml. of 1:1 HCl, the salt being about 10 years old and badly oxidized. The solution was found to contain 68% of stannous and 32% of stannic tin.

(2) By preparing a similar solution from fresh stannous chloride of good appearance. This contained 93% of stannous and 7% of stannic tin.

(3) By dissolving 8.4 g. of tin in 32 ml. of conc. HCl and 8 ml. of water, adding two drops of 5% copper sulphate to assist solution. On test, this preparation was found to contain 100% stannous tin.

From each of these, diluted solutions of the same stannous tin content were made, in water and in 5% v/v HCl, and were used for reagent blank determinations. The results are shown in Table II.

From these it appears that in solutions diluted with water, high stannic tin content is accompanied by high reagent blank values. When hydrochloric acid is used the blanks appear to be independent of the stannic tin concentration. It is notable that even in the case of the reagent prepared by diluting the 100% stannous chloride with water there is an enhanced extinction, which may be due to the production of sufficient stannic tin in the diluted solution to cause some scattering of light.

After this demonstration that the reagent blank is increased in distilled water if the stannous chloride reagent has a low HCl content and high stannic tin concentration, the effect in sea water was measured. The experiments were carried out under the same conditions as are used when phosphate in sea water

TABLE II. EFFECT OF VARYING STANNIC TIN CONTENT OF STANNOUS CHLORIDE REAGENT UPON REAGENT BLANK

Fraction of total tin content of stock solution in		Stock solution diluted with water		Stock solution diluted with 5 % v/v HCl	
Stannous form (%)	Stannic form (%)	Extinction	Reagent blank (mg./m. ³)	Extinction	Reagent blank (mg./m. ³)
68	32	0.023	2.7	0.009	1.1
		0.029	3.4	0.008	1.0
93	7	0.024	2.8	0.007	0.8
		0.022	2.6	0.008	1.0
100	Nil	0.018	2.1	0.009	1.1
		0.019	2.3	0.008	1.0

is determined, viz. to 67 ml. of sea water 3 ml. of a reagent containing 18% v/v H₂SO₄ and 10.7% ammonium molybdate were added. The extinction of the resulting solution was measured. Three drops of stannous chloride were added, and the extinction again measured when it had attained its maximum. To the solution 0.3 ml. of a standard phosphate solution was then added, increasing the phosphorus concentration by 20 mg. per m.³, followed by a further two drops of stannous chloride. The extinction was measured again when it had reached its maximum. The difference between the first two readings was a measure of the phosphate-phosphorus content of the sea water, together with the blank contributed by the reagents. The difference between the second and third readings measured the extinction produced by unit quantity of phosphorus under the experimental conditions. A separate determination of the reagent blank allowed the phosphate-phosphorus content of the sea water to be calculated.

Table III shows results obtained with a sample of sea water of low phosphate content which had been filtered to remove any particulate matter which might contain phosphate (Cooper, 1948, p. 298).

Although in absence of sufficient hydrochloric acid it is seen that the increase in extinction is enhanced by the presence of stannic tin, this enhancement is less in sea water than in distilled water; it has led in the extreme case to a negative value for the calculated phosphate-phosphorus. No significant alteration is seen in the extinction recorded after addition of phosphate subsequent to the first measurement.

The experiment was duplicated with the same sea water enriched with 8.9 mg./m.³ of phosphate-phosphorus. The stannous chloride solutions in this experiment were different preparations. The results are shown in Table IV.

The difference in extinction values for the addition of 20 mg./m.³ phosphate-phosphorus between Tables III and IV can be accounted for by the temperature difference.

TABLE III. ESTIMATION OF PHOSPHATE IN SEA WATER USING STANNOUS CHLORIDE REAGENTS CONTAINING EQUAL QUANTITIES OF STANNOUS, AND VARYING AMOUNTS OF STANNIC TIN. TEMPERATURE OF SOLUTIONS, 22° C.

Stannic tin content of stock solution as fraction of total tin present (%)	Stock solution diluted with water				Stock solution diluted with 5 % v/v HCl			
	Extinction in		Further increase in extinction in sea water after subsequent addition of 20 mg./m. ³ phosphate-P	Calculated PO ₄ -P (mg./m. ³)	Extinction in		Further increase in extinction in sea water after subsequent addition of 20 mg./m. ³ phosphate-P	Calculated PO ₄ -P (mg./m. ³)
	Distilled water	Sea water			Distilled water	Sea water		
67	0.068, 0.069	0.037 0.039	0.168 0.172	-3.8 -3.4	0.011, 0.010	0.031 0.033	0.170 0.168	2.4 2.6
32	0.030, 0.030	0.043 0.040	0.170 0.172	1.5 1.2	0.010, 0.009	0.030 0.030	0.171 0.169	2.4 2.4
Nil	0.016, 0.015	0.031 0.033	0.167 0.169	1.9 1.9	0.010, 0.010	0.031 0.033	0.170 0.168	2.5 2.6

TABLE IV. ESTIMATION OF PHOSPHATE IN SEA WATER ENRICHED WITH 8.9 MG. PHOSPHATE-P PER M.³ USING STANNOUS CHLORIDE REAGENTS CONTAINING EQUAL QUANTITIES OF STANNOUS, AND VARYING AMOUNTS OF STANNIC TIN. TEMPERATURE OF SOLUTIONS, 20° C.

Stannic tin content of stock solution as fraction of total tin present (%)	Stock solution diluted with water				Stock solution diluted with 5 % v/v HCl			
	Extinction in		Further increase in extinction in sea water after subsequent addition of 20 mg./m. ³ phosphate-P	Calculated PO ₄ -P (mg./m. ³)	Extinction in		Further increase in extinction in sea water after subsequent addition of 20 mg./m. ³ phosphate-P	Calculated PO ₄ -P (mg./m. ³)
	Distilled water	Sea water			Distilled water	Sea water		
59	0.042, 0.032	0.107 0.108	0.166 0.167	8.4 8.5	0.010, 0.010	0.107 0.107	0.167 0.168	11.6 11.6
32	0.030, 0.030	0.111 0.116	0.167 0.168	9.7 10.2	0.011, 0.011	0.109 0.109	0.167 0.168	11.7 11.7
Nil	0.014, 0.013	0.108 0.107	0.167 0.167	11.2 11.1	0.009, 0.009	0.107 0.107	0.168 0.168	11.7 11.7

The last columns of these tables, showing the calculated phosphorus in the sea water without and with the addition of 8.9 mg./m.³, show a mean difference of 9.18 mg./m.³ with a maximum difference of 9.3 and a minimum difference of 9.0. This estimated difference is considered to be in reasonable agreement with the known addition of phosphate, and indicates that the technique of 'subsequent addition' is valid (Harvey, 1948, p. 351).

It is therefore recommended that the stannous chloride used in this method should contain at least 5% by volume of concentrated hydrochloric acid.

This condition, it should be noted, is complied with in the original visual method of Atkins (1923, p. 144), in which the freshly prepared stannous chloride contains 10 to 20% by volume of acid. In any event the presence of stannic tin with a low acid concentration is less likely to upset the visual estimation of the reagent blank, as its effect is to discolour, not augment, any blue colour formed.

SUMMARY

The results of phosphate determinations in sea water by the Denigès method, using red light, in an absorptiometer, may be in error if the stannous chloride reagent has low HCl concentration, and contains stannic tin.

The error is in the reagent blank determination, and seems to be caused by colloidal stannic compounds which increase the opacity of the solution. In sea water the effect may be smaller or immeasurable so that results are over-corrected.

When the stannous chloride solution contains about 5% hydrochloric acid, reagent blank figures are low, and independent of stannic tin concentration. This acidity is recommended.

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THE SEASONAL ABUNDANCE OF YOUNG FISH

X. THE YEAR 1948

By P. G. Corbin, B.A.

Zoologist at the Plymouth Laboratory

(Text-figs. 1-2)

Records of the young fish and plankton of Plymouth off-shore waters taken in $\frac{1}{2}$ hr. oblique hauls of the 2 m. stramin ring-trawl were continued in 1948. They show an even lower production of young fish than in 1947 and a continued poverty of plankton organisms other than young fish. The dates on which collections were made are given in Table I.

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1948

All 2 miles east of Eddystone, unless otherwise stated

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
6	3	1	12*	19	1	5	4	6	4*	4	6
14	9	11†	14	25	7	12	9	13	7	9	15
20	12*	11*			8*	19	18	20	12	16	20
26	16	15			14	26	23	28	21	22	
		23			21	29*	30		26	29	
							31*		27*	30*	

* Station E 1.

† Station L 4.

TABLE II. FORTNIGHTLY AVERAGE CATCHES OF ALL YOUNG FISH EXCLUDING CLUPEIDS, 1930-34, 1947 AND 1948

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1930-34* 1st fortnight	5	10	27	110	635	299	100	152	48	11	7	2
average) 2nd fortnight	8	15	89	374	573	78	85	48	9	6	3	2
1947 1st fortnight	n.r.	5	6	5	n.r.	20	10	11	11	2	1	+
2nd fortnight	0	43	13	10	54	27	5	16	1	0	+	+
1948 1st fortnight	+	3	15	12	n.r.	13	9	9	+	4	0	1
2nd fortnight	0	16	15	n.r.	65	32	17	5	0	+	+	0

* Data kindly supplied by Mr F. S. Russell.

n.r., no records. + average of less than 1.

The fortnightly averages of all young fish, excluding clupeids, are now too low to be graphed against the same averages for the period 1930-34 as in Fig. 1 of former reports: they are therefore given numerically in Table II below, with the 1947 averages for comparison. *Callionymus* spp. and *Solea variegata* contributed principally to the highest of these fortnightly averages in the

second half of May; the next highest value in the second half of June was also mainly due to *Callionymus* spp.

Earlier parts of this series (Russell, 1930-47; Corbin, 1948) also give a table of the monthly average catches of young fish. These have now fallen to so low

TABLE III. MONTHLY TOTAL CATCHES OF POST-LARVAE PER HALF-HOUR
OBLIQUE HAULS WITH 2 M. STRAMIN RING-TRAWL, 1948

The number of hauls per month is shown by the small figure against each month at the head of the column. A + is used in the 2nd, 4th and 6th lines to denote monthly average of less than 0.5.

A + is used in the 2nd, 4th and 6th lines to denote monthly average of less than 0.5.														Sum of monthly averages
	Jan. ⁴	Feb. ⁴	Mar. ⁵	Apr. ²	May ²	June ⁵	July ⁵	Aug. ⁴	Sept. ⁴	Oct. ⁶	Nov. ⁶	Dec. ³	Total	
Total young fish	4	107	406	27	149	198	162	83	6	151	1	5	1299	..
Monthly average, T.Y.F.	1	27	81	14	75	39	32	14	1	25	+	2	..	331
T.Y.F., less Clupeids	1	26	74	23	130	83	70	39	2	14	1	3	466	..
Monthly average, ditto	+	6	15	12	65	17	14	6	+	2	+	1	..	138
All Clupeid spp.	3	81	332	4	19	115	92	44	4	137	0	2	833	..
Monthly average, ditto	1	20	66	2	10	23	18	7	1	23	0	1	..	172
<i>Clupea harengus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Gadus pollachius</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Gadus merlangus</i>	..	..	1	1	5	4	2	..	..	..	..	..	13	4.4
<i>Gadus minutus</i>	..	..	7	1	..	..	..	..	..	..	..	..	8	1.9
<i>Gadus luscus</i>	1	..	16	..	..	..	..	..	..	..	1	1	19	3.45
<i>Gadus callarias</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Onos</i> spp.	..	..	..	5	20	2	..	..	..	..	..	..	27	12.9
<i>Phycis blennioides</i>	..	..	..	..	..	..	..	..	..	..	..	..	1	0.3
<i>Molva molva</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Merluccius merluccius</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Raniceps raninus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Capros aper</i>	..	..	..	..	..	..	..	..	..	1	..	..	1	0.17
<i>Zeus faber</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Arnoglossus</i> spp.	..	..	..	..	..	13	11	..	7	..	..	..	31	5.57
<i>Rhombus</i> spp.	..	..	..	..	6	6	1	3	..	..	4	..	4	0.7
<i>Scophthalmus norvegicus</i>	..	..	..	..	..	1	..	..	..	..	..	..	12	4.2
<i>Zeugopterus punctatus</i>	..	..	..	..	..	1	..	..	..	..	..	..	1	0.2
<i>Zeugopterus unimaculatus</i>	..	..	..	..	..	2	..	..	..	..	..	..	2	0.4
<i>Pleuronectes platessa</i>	..	..	13	..	..	..	..	..	..	..	..	..	13	2.6
<i>Pleuronectes limanda</i>	..	..	..	..	5	1	..	..	..	..	..	..	6	2.7
<i>Pleuronectes flesus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Pleuronectes microcephalus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Solea vulgaris</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Solea variegata</i>	..	..	..	..	33	2	..	..	..	..	..	..	35	16.9
<i>Solea lascaris</i>	..	..	..	..	..	..	1	2	..	1	..	..	4	0.7
<i>Solea lutea</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Seranus cabrilla</i>	..	..	..	..	..	..	1	..	..	..	..	..	1	0.2
<i>Caranx trachurus</i>	..	..	..	..	..	..	9	4	..	2	..	..	15	2.8
<i>Mullus surmuletus</i>	..	..	..	..	..	..	1	..	..	..	..	..	1	0.2
<i>Morone labrax</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Ammodytes lanceolatus</i>	..	..	..	5	1	2	4	..	..	..	..	..	12	4.2
<i>Ammodytes tobianus</i>	..	..	..	1	..	..	1	..	..	..	..	..	2	0.7
<i>Ammodytes marinus</i>	..	..	..	1	..	..	..	..	..	..	..	..	1	0.5
<i>Ammodytes</i> sp. IV	..	12	13	2	..	..	..	..	..	..	..	..	27	6.6
<i>Cepola rubescens</i>	..	..	..	..	..	..	..	1	1	..	..	..	2	0.42
<i>Callionymus</i> spp.	..	..	2	7	60	27	8	4	..	1	..	..	109	41.6
<i>Labrus bergylta</i>	..	..	..	..	..	2	1	..	..	..	..	..	3	0.6
<i>Labrus mixtus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Ctenolabrus rupestris</i>	..	..	..	..	..	20	12	1	..	..	..	..	33	6.57
<i>Crenilabrus exoletus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Trachinus vipera</i>	..	..	..	..	..	..	1	3	..	..	..	..	4	0.7
<i>Scomber scombrus</i>	..	..	..	..	..	..	3	1	..	..	..	..	4	0.77
<i>Gobius</i> spp.	..	1	..	..	..	4	3	1	1	..	..	..	10	2.07
<i>Lebetus scorpioides</i>	..	..	..	..	..	..	1	1	..	..	..	..	2	0.37
<i>Blennius ocellaris</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Blennius pholis</i>	..	..	..	..	..	..	..	1	..	..	..	..	1	0.17
<i>Blennius gattorugine</i>	..	..	..	..	..	9	6	5	..	..	..	..	20	3.8
<i>Chirolophus galerita</i>	..	13	18	..	..	..	..	..	..	..	..	..	31	6.85
<i>Mugil</i> spp.	..	..	..	..	..	..	..	..	..	..	..	1	1	0.33
<i>Agonus cataphractus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Trigla</i> spp.	..	..	3	..	..	1	..	..	..	..	..	..	4	0.8
<i>Cottus</i> spp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Liparis montagui</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Lepadogaster bimaculatus</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Lophius piscatorius</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pipe fish	..	..	1	..	..	..	2	1	..	2	..	..	6	1.1
													466	138

a level for almost all species that it is considered more informative to show the monthly total catches for species (Table III) rather than the monthly average catches, many of which are now considerably less than one. For comparison with previous records, the sums of the monthly averages for the year are given in the last column of this table, and the monthly averages of (i) total young fish, (ii) total young fish less clupeids, and (iii) total clupeids are also shown (2nd, 4th and 6th lines, in black). The number of hauls per month is included so that the monthly averages for the species are immediately derivable.

A few young plaice, *Pleuronectes platessa*, again occurred this year, in March. A single specimen of *Mugil* spp. was taken on 15 December: in 1947 another single specimen was caught at E 1, on 13 November (this haul was not included in the 1947 data).

A young specimen (33 mm.) of *Phycis* was also taken in the haul of 15 December this year. It very probably belongs to *P. blennioides* as this is the only *Phycis* species occurring in the area. No young stages of this genus have previously been recorded off Plymouth.

As already mentioned, plankton other than young fish was very scarce throughout the year. The maximum haul of *Calanus* (adult and stage V) contained 280 odd specimens (1 June 1948), and only four other catches during the year contained more than 100 *Calanus*. This, when compared with the rich catches of 1930 (Russell, 1933), gives some indication of the present poverty. In 1930, thirty-four of the forty-four hauls taken during the year contained more than 100 *Calanus* and seventeen out of the forty-four had catches of over 1000: the maximum haul contained the very large total of 318,450 specimens (7 May 1930).

Sagitta setosa was the dominant *Sagitta* species throughout the year (Figs. 1 and 2). It was, however, considerably less numerous than in 1947: on only two occasions were catches of more than 1000 taken (1 March, 31 August; 1200 odd). As in 1947, it was almost completely absent during the period April–July. The occurrence of *S. elegans* was very intermittent during the year and the numbers caught were extremely small (maximum, ten specimens).

A particularly noticeable feature of the *S. setosa* catches throughout the year was the preponderance of very small immature specimens (Stages I and II; Russell, 1932*a*). This departure from the normally expected proportions of development Stages (I–III) in the catches would appear to indicate an unusually low survival of individuals reaching maturity. Measurements and counts, comparable with those made by Russell (1932*b*), are required for verification of this trend. It is, however, felt that it should not remain unrecorded, since it may possibly represent a further aspect of the continued and progressive impoverishment of the macroplankton caught by the 2 m. ring-trawl in this area.

Except during April, *Muggiaea atlantica* was present during all months of

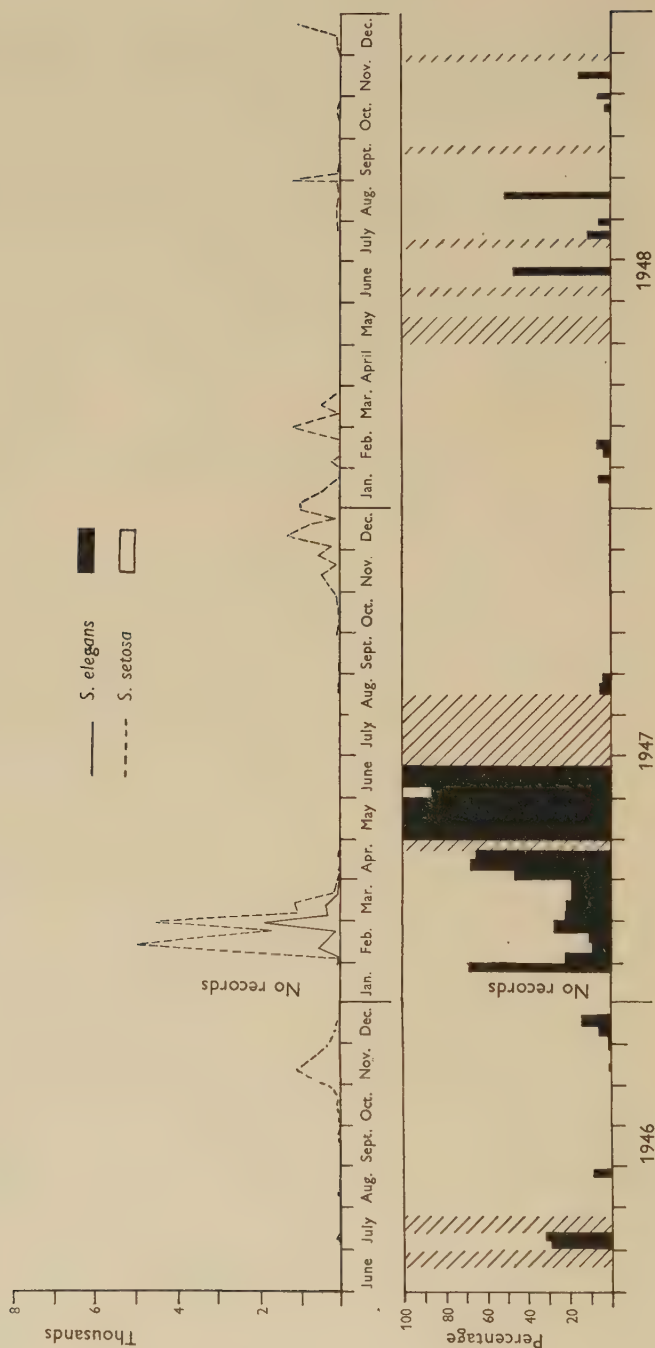


Fig. 1. Above, curves showing the actual abundance of *Sagittia elegans* (—) and *S. setosa* (----) in half-hour oblique hauls with the 2 m. stramin ring-trawl during the period June 1946 to December 1948. Below, percentage composition of the *Sagittia* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagittia*, hatched. (Continued from Corbin, 1948, p. 720, fig. 2.)

the year: it was numerous from the end of July until the end of August and again from the end of September until the end of October.

M. kochi, which was present in very small numbers in 1946 (Russell, 1947) but did not occur in 1947 (Corbin, 1948), was also represented in the catches throughout the year except during February and April. It did not generally exceed one-third of the numbers of *M. atlantica*. In the earlier part (January-June) and at the end of the year (November and December), the catches of both *Muggiaea* species were small.

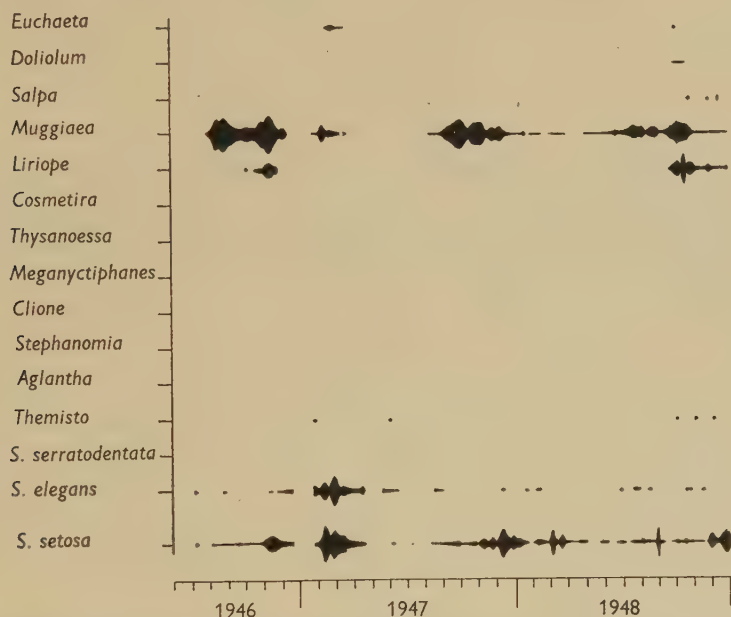


Fig. 2. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the period June 1946 to December 1948. (Continued from Corbin, 1948, p. 721, fig. 3.)

At the end of September (28th), *Liriope* appeared in considerable numbers. It continued until the end of the year in the catches, although only in small numbers in November and December.

Salps occurred on three occasions (27 October (35), 30 November (1), 15 December (69)), and doliolids were taken twice in October (4th (25), 21st (3)).

Three specimens of *Euchaeta hebes* also occurred in the catch of 4 October, and the hyperiid amphipod, *Themisto* was present in three hauls at the end of the year (4 October (1), 4 November (11), 6 December (1)).

Beroe was present during October, November and December, and *Aequorea pensilis* occurred in some numbers during November and December. Mr F. S. Russell kindly identified the *Aequorea* specimens.

TABLE IV. PILCHARD EGG CATCHES, 1948

See Table I for dates of hauls.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
0	0	0	17	3,160	1,860	1,300	0	0	57	1	0
0	0	0	11	1,450	3,000	5	0	104	6	0	3
1	0	2			7,980	103	0	14	7	4	1
0	0	0			6,880	40	0	240	132	0	
		1			2,100	0	0		10	0	
							0		0	4	
Monthly average, 1948	+	0	+	14	2,305	4,364	290	0	89	35	+
Monthly average, 1937-9 and 1946-7*	+	0	+	478	5,868	14,093	6,196	385	415	305	398

* Calculated from data in previous reports of this series.
+ Average of less than 10.

Pilchard eggs were taken during all months of the year except in February and August. Their occurrences are given in Table IV. The average catch in June, the month of maximum pilchard spawning in this area, was very considerably lower than in previous years.

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A QUANTITATIVE METHOD FOR ESTIMATING THE PERIODICITY OF DIATOMS

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(Plate I and Text-fig. 1)

INTRODUCTION

The method described below was evolved as a substitute for counting, which is unsatisfactory for epiphytic marine diatoms. It depends upon the estimation of the amount of diatom-silica associated with unit dry weight of the substratum. The sea-weed samples are first freed from sand particles and are then treated with strong nitric acid in the usual way. In order to convert the insoluble silica of the diatoms into a soluble form suitable for chemical estimation, the material is fused in a platinum crucible with a mixture of K_2CO_3 and Na_2CO_3 and the fused mass is dissolved in (silica-free) distilled water and filtered. The amount of silica in the filtrate is determined colorimetrically according to the method of Dienert and Wandenbulcke (cf. Atkins, 1926). The method is simple in practice and saves considerable time and labour. The full procedure is illustrated by reference to a study of the periodicity of *Grammatophora marina* (Lyngb.) Kütz. at Swanage, Dorset.

This species (Pl. I) is found all the year round on *Cladophora rupestris* in a pit in one of the reefs at Peverel Point, Swanage. In summer it is the only epiphytic diatom on the *Cladophora*, while in spring and autumn small numbers of other epiphytes (*Cocconeis*, *Opephora*, *Rhoicosphenia*) are present. In order to obtain a fairly representative picture of the abundance of *Grammatophora* at different times, samples of the *Cladophora* were collected monthly from a definite area in the pit, each including 3-4 cm. of the apices of five to ten *Cladophora* tufts cut at random. The tufts are soaked in sea water to free them from sand particles and preserved in 4% formalin.

METHOD OF ESTIMATION

After soaking in several changes of distilled water, the sample is transferred to a small crucible and dried in an electric oven at $100^\circ C$. for several hours; the crucible is then allowed to cool in a desiccator. When a constant weight has been attained, the contents of the crucible are boiled with concentrated nitric acid until all the organic matter is destroyed, as shown by the addition

of a few crystals of potassium chromate. The remaining material is washed thoroughly with water, and subsequently repeatedly washed with alcohol or ether. After drying it is mixed with about twenty times its volume of K_2CO_3 and Na_2CO_3 , in the proportions of 2:1, and the mixture is fused in a platinum crucible over a strong Bunsen flame for at least 20 min., care being taken to avoid a smoky flame. The melting-point is lowered by using the two carbonates.

After fusion is complete, water from a tap is allowed to play on the hot crucible in order to prevent the contents from adhering to the sides. The fused mass is then dissolved in warm distilled water and the solution filtered. If fusion has been carried out properly, no appreciable residue remains. The filtrate is diluted to 50 ml. with distilled water and shaken. According to the concentration of silica present, 1–5 ml. of this solution are pipetted into clean pyrex tubes, again diluted to 50 ml. and the amount of SiO_2 in the final solution determined colorimetrically. For each determination 2 ml. of a 10% solution of ammonium molybdate and four drops of 50% (by volume) sulphuric acid are required. After adequate stirring an intense yellow colour appears within 2–5 min. at 20–25° C. and this colour is matched with a standard colour produced by a known concentration of silica. For this purpose a set of B.D.H. 'V.H.B.' tinometer disks was used. The matching of the colour was carried out in daylight in front of a north window. The yellow colour is produced only within a certain range of pH (the resulting mixture should be close to pH 2), and one more drop of acid may suppress it altogether. Phosphates and arsenates give the yellow colour only when present in large amounts, but the diatom does not contain them. Errors in the chemical estimation of the silica owing to incomplete fusion or to incomplete production of colour during the colorimetric tests are easily avoided. The same interval of time was always allowed to elapse between adding the reagents and carrying out the tests which were always performed at approximately the same temperature.

For computing the amount of SiO_2 per gram dry weight of the *Cladophora* the following equation is used:

$$x = \frac{50e}{w},$$

where x is the unknown quantity (in mg.) of silica found in 1 g. dry weight of *Cladophora*, e the actual amount (in mg.) of silica present in 1 ml. of the filtrate as estimated with the tintometer, and w is the actual dry weight of the sample in grams. w includes the dry weight both of the substratum and of the epiphyte, but since that of the latter is negligible in comparison with that of the former a correction was deemed unnecessary. If sand is present, the cleaned diatom-material is well shaken in water, the liquid allowed to stand until the sand has settled and the supernatant liquid containing the diatoms poured off and centrifuged. The sandy sediment is dried and weighed, and the weight subtracted from the initial dry weight of the sample.

The results of a series of estimations are given in Table I.

TABLE I. ABUNDANCE OF *GRAMMATOPHORA MARINA* ON *CLADOPHORA* AT SWANAGE, EXPRESSED IN MG. OF SiO_2 PER GRAM OF DRY WEIGHT

Date	SiO_2
1947 April	80.0
May	58.8
July	17.6
August	12.7
September	26.6
December	21.7
1948 January	37.8
February	88.1
March	34.5

COMPARISON WITH THE COUNTING METHOD

The accuracy of the method was tested by counting the individuals of *Grammatophora* present in the samples (Table II). The cleaned diatom material was diluted with a definite volume of water, depending upon the density of the sample. After thorough shaking, a ml. at a time of the suspension was pipetted into a counting cell, ruled into 1 and $\frac{1}{16}$ mm. squares (corresponding to volumes of 1 mm.³ and $\frac{1}{16}$ mm.³ respectively), and holding just 1 ml. when covered with a cover-glass. According to the density of the sample, counts were made either, under low power, of the number of frustules in a square millimetre or, under high power, of the number within the field of the microscope. The squares or fields were chosen at random, the number counted ranging between 4 and 88. Half frustules were counted as such, although it was sometimes difficult, especially under low power to distinguish them from whole ones. After making the counts the contents of the cell were carefully washed back into the original suspension to be used for the fusion tests.

In computing the total number of frustules of *Grammatophora* per gram of dry weight of *Cladophora* in a sample the following formula was used

$$n = \frac{n_1 \times v \times 10^3}{w},$$

where n is the total number per gram dry weight; n_1 is the average number of frustules in a cubic millimetre of the counting cell, v the volume in ml. of the diluted diatom-material and w the actual dry weight in grams of the original *Cladophora* material. This gives the number of individuals of *Grammatophora marina* per gram dry weight of *Cladophora* in April 1947 as

$$\frac{193.6 \times 25 \times 10^3}{0.5} = 9.68 \times 10^6$$

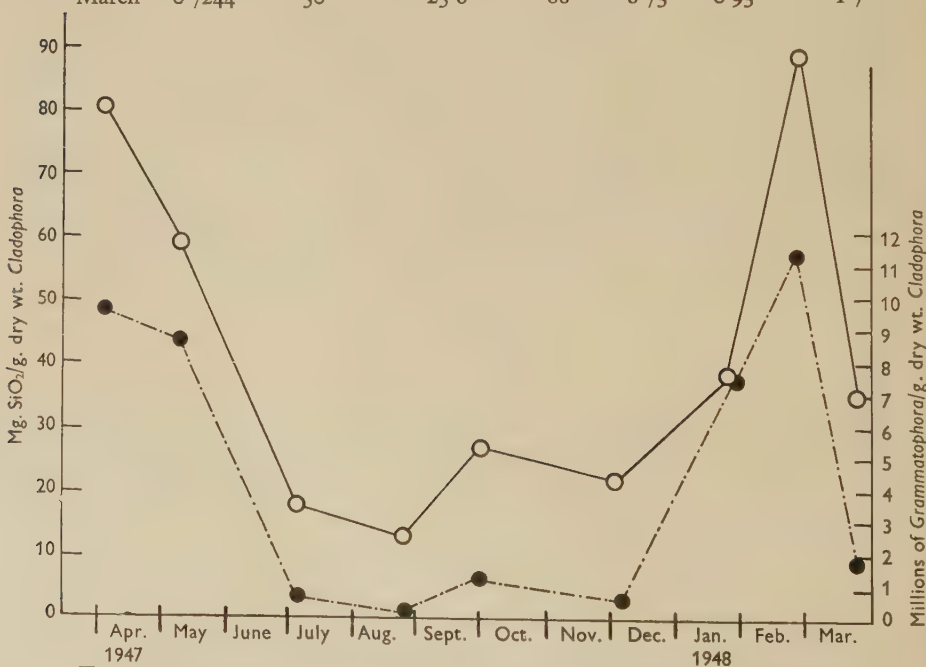
approximately.

The degree of abundance of *Grammatophora marina* in successive months, as determined by the two different methods, is shown graphically in Text-fig. 1.

The two graphs run almost exactly parallel and show clearly that *G. marina* has a pronounced maximum in early spring and a secondary one in autumn. Comparing the graphs and bearing in mind that they are drawn to different scales, that based on the silica content of the samples is relatively flat, the range of values being comparatively low. The amount of silica in the diatom material at the time of maximum abundance in February 1948 is only about seven times that found at the time of the minimum in August 1947, while the

TABLE II. COMPUTATION OF THE PERIODICITY OF *GRAMMATOPHORA* IN THE *GRAMMATOPHORA-CLADOPHORA* COMMUNITY AT SWANAGE BY THE COUNTING METHOD

Date	Dry wt. of material (g.)	Volume of diluted material (ml.)	Average no. of individuals per 1 mm. ² of the counting cell	No. of counts	σ	σ_{mean}	Total no. of individuals per g. dry wt. of material ($\times 10^6$)
1947 April	0.5000	25	193.6	14	57.41	15.34	9.68
May	0.5130	23	196.8	15	96.28	24.86	8.8
July	0.3922	28	10.0	4	3.7	1.85	0.7
Aug.	0.4374	23	1.5	16	1.07	0.27	0.08
Sept.	0.4360	30	18.0	13	1.86	0.52	1.2
Dec.	0.2303	46	3.2	15	2.18	0.56	0.64
1948 Jan.	0.7940	46	128.0	35	53.52	9.04	7.4
Feb.	0.6810	50	152.0	76	29.67	3.4	11.2
March	0.7244	50	25.6	88	8.73	0.93	1.7



Text-fig. 1. Periodicity of *Grammatophora marina* during 1947-48, as computed by: (a) the silica-content method (—); (b) the counting method (---).



Fig. 1.

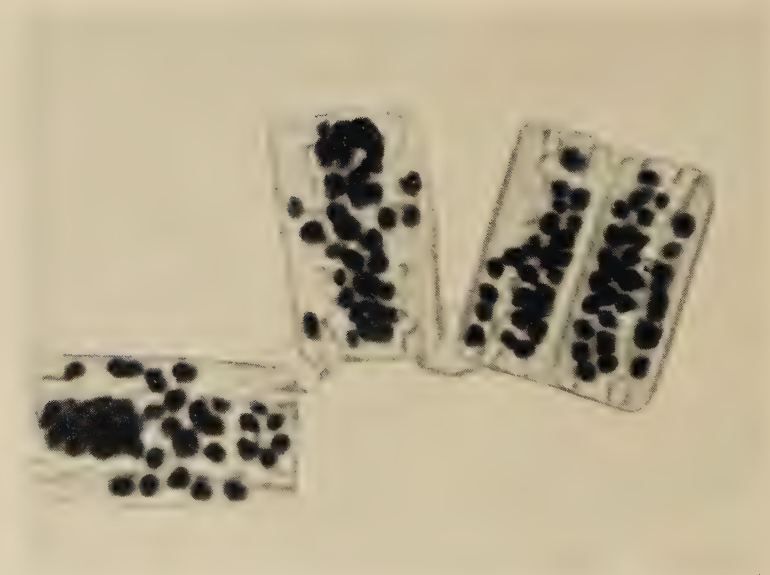


Fig. 2

counting method shows the ratio of the numbers of frustules on these two dates to be about 100:1. The discrepancy is due to the fact that the amount of silica is not actually proportional to the numbers of frustules, but to their total surface area.¹ At certain times, and especially when there is abundant multiplication, the individuals may be very small, a considerable number being only about one-quarter of the usual length. The occasional inclusion of a half as a whole frustule during counting is another cause for the discrepancy between the results of the two methods.

DISCUSSION

The ability of a diatom to assimilate silica from the medium and produce new frustules during multiplication affords a measure of its rate of growth. The total amount of growth at a given time will be represented by the quantity of silica present. The silica method is comparable to the pigment-extract method used by Harvey (1934), in which the amount of pigment extracted from a known volume of sea water is taken to indicate the quantity of phytoplankton present. The silica method, on the other hand, can be regarded as specific for diatoms.

The amount of silica in the diatom material can be expressed in terms of unit weight, unit area or unit volume of the medium or substratum. The method can therefore be used for determining the periodicity of planktonic, lithophytic (e.g. *Schizonema*) or epiphytic diatoms. The samples must not, however, contain other organisms having a siliceous envelope (e.g. Silicoflagellates).

The method is open to the criticism that the degree of silicification of the frustules of a given species of diatoms may not be the same at all times of the year or in individuals of different sizes. There is at present no accurate information on this matter, but it seems probable that the amount of silicification is constant in most species, judging from observations made at different times.

I am indebted to Prof. F. E. Fritsch, F.R.S., and to Dr W. R. G. Atkins, F.R.S., for valuable advice and criticism, and to Dr F. M. Haines for reading the manuscript.

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EXPLANATION OF PLATE I

Fig. 1. Photomicrograph of the *Cladophora-Grammatophora* community.

Fig. 2. Part of the colony of *Grammatophora marina* shown above, enlarged.

¹ It is assumed that the frustules are uniformly silicified and that the thickness of the valves is the same whatever the size.

CASCADING OVER THE CONTINENTAL SLOPE OF WATER FROM THE CELTIC SEA¹

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(Text-figs. 1-14)

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This paper is an essay on the theme that water, cooled in winter, will sink and flow downhill over the sea floor. It will be shown that in some winters water in the Celtic Sea to the south of Ireland became heavy enough to flow to the edge of the continental shelf and there to sink to a depth of several hundred metres. It will be shown, further, that in one year it actually did so. A theory of this phenomenon, termed 'cascading', has been developed, and implications capable of test by observation are discussed.

INTRODUCTION

A better understanding of the oceanography of the English Channel requires a fuller knowledge of the nature of the movements of water within the Celtic Sea, and of the water which enters or leaves the ocean over the Continental Slope. This need has been strengthened by the demand from the fishery naturalists for a statement of the physical and chemical conditions in the Celtic

¹ For a definition of the name 'Celtic Sea', see Appendix, p. 750.

Sea during the mackerel investigations of 1937-39. In that area, and in the English Channel, attempts to correlate the distribution of plants, animals and chemical nutrients on the one hand with salinity and currents deduced from salinity and temperature diagrams on the other have been singularly barren. No correlation such as that between the winter maximum phosphate and the distribution of young fish has ever emerged.

This negative result has become so definite that it can have but one meaning; the presence of waters with similar salinities but very different physical and biological histories. Comparative study of the ocean water to the west and south-west seems essential. It would appear that there are three types of high-salinity water in the area: (a) North Atlantic Central water, with a well-defined temperature-salinity relation occupying the upper 600 m. well to the west and south-west; (b) the Mediterranean tongue between 800 and 1200 m. with a salinity in excess of 35.5‰ and $67\text{--}70\text{‰}$ saturated with oxygen, which may possibly, under certain conditions, be projected on to the continental shelf; and (c) 'cascade'¹ water formed by winter cooling of high-salinity waters on the banks to the west and south of Ireland with a salinity usually over 35.4‰ and an oxygen content over 90‰ saturated. Since the problems are very complex, a complete and polished account must take many years to prepare. Here an attempt is to be made to dissect a single factor from the matrix of events; a final assessment of its importance relative to others must wait. The paper is an attempt to achieve a better understanding of exchanges between shelf and ocean for which Iselin (1940) so cogently argues.

It is widely recognized that the cold, dense abyssal waters of the ocean are formed in the Weddell Sea (Deacon, 1937), south-east of Greenland and to some extent in the Norwegian Sea (Nansen, 1912). In marked contrast the contribution to the intermediate layers of the oceans made by winter cooling of water over the extensive continental shelves in mid-latitudes has been neglected. None the less, the effect upon the oceans on the one hand and upon the productivity of fishing grounds on the other may well be profound. In this paper, therefore, the effect upon circulation in the Celtic Sea and the adjacent ocean of the increase in density of shelf water south of Ireland in winter is to be discussed.

PRESENT VIEWS OF CIRCULATION IN THE CELTIC SEA

The account given by Matthews (1914) remains unchallenged. In general, a current of salt warm water enters the English Channel from a south-westerly direction and in part turns northwards and north-westwards to escape into the Irish Channel. Part again follows the south coast of Ireland and, on occasion, there may be a centre to the cyclonic eddy in about 51°N. , $6^{\circ}40'\text{W.}$ It may be said at once that nothing here to be presented is in conflict with Matthews' account of a cyclonic circulation.

¹ A very descriptive term due to Mr G. A. Steven.

THEORY OF CASCADING¹

In autumn and winter heat is lost from the surface of the sea mainly by radiation and evaporation. To a first approximation the extent to which this happens is directly dependent on the area of sea surface.

Let us consider two positions in winter, A and B (Fig. 1), having the same initial salinity, temperature and density, and exposed to similar meteorological conditions; at B the water is twice as deep as at A. If at B purely vertical mixing is sufficient to equalize the temperature there, the fall in temperature will be only half as great as at A. Although at both positions the loss of heat through the surface is much the same, at B, it would be distributed through twice the depth as at A. Since at A the water has become not only colder but heavier, it will tend to cascade or flow downhill along the bottom from A to B.

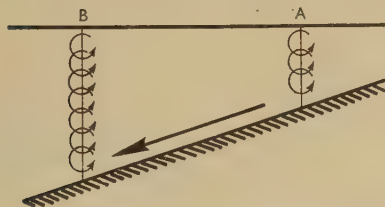


Fig. 1. The basis of cascading

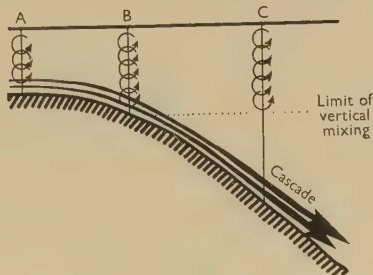


Fig. 2. Cascading over the Continental Slope.

Although in an enclosed tank the result would be an isothermal and completely uniform body of water in which it would be impossible to separate downhill movement from purely vertical mixing, in nature this need not be so.

Let us consider the edge of the continental shelf above the continental slope (Fig. 2). At the inshore and shallower station A the water should be cooled to a greater extent than at the deeper station B. In consequence a bottom or cascade current should become established from A to B. All the time straight-forward vertical mixing due to wind and cooling *in situ* will be occurring down to the depth of maximum vertical mixing. The combined result should be a current setting from A through B with its greatest strength near the bottom. When the bottom current approaches the edge of the slope there should come a depth to which vertical mixing could no longer reach as indicated by the dotted line near station C. It would, however, continue to cascade as a heavy

¹ After we had received proofs of the present paper, we saw, unfortunately, for the first time, a paper by Fridtjof Nansen (1913), describing the effect of winter cooling over the Rockall Bank and the descent of the resulting heavy water over the adjacent slope. Nansen has given a complete description of cascading there. Since the importance of his concept, as applied in temperate latitudes would seem not to have been widely recognized and accepted, a completely independent derivation and application in another area, accompanied by further deductions, may not prove unwelcome. Accordingly no alteration has been made in the present text.

relatively cold blanket of water until it should reach such a depth on the wall of the slope as would correspond to the density of the neighbouring ocean water. In a cold winter this depth would evidently lie deeper than in a mild one.

Since the cascaded water has to be replaced, somewhere or other compensation water must break in, most probably from the ocean. This theme will be more fully discussed on pp. 735-40.

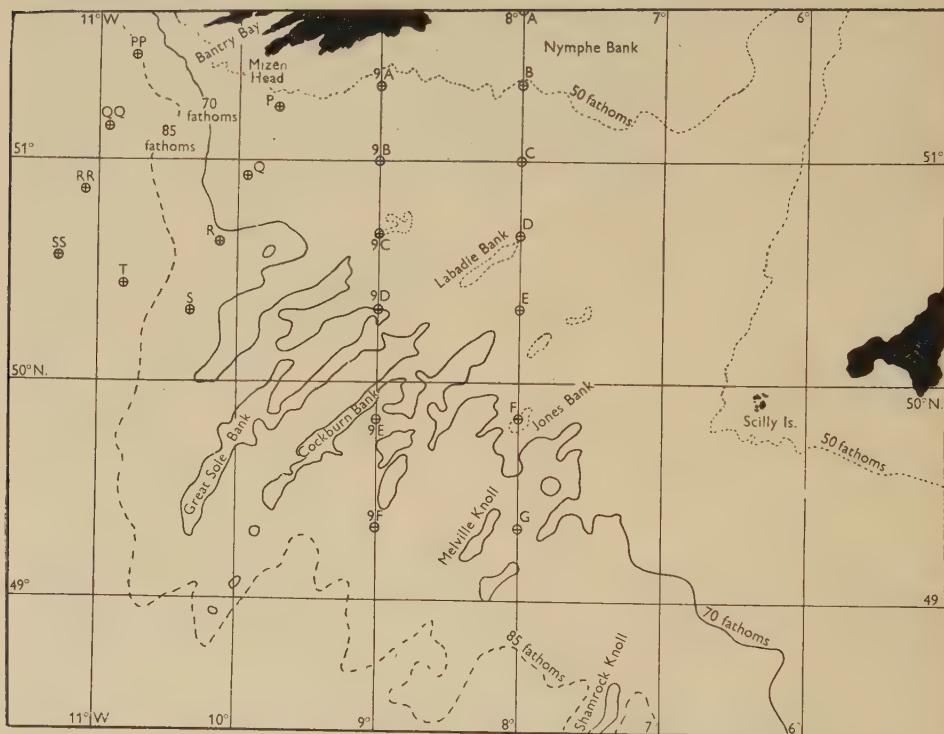


Fig. 3. Submerged 'river valleys' as revealed by the 70 and 85 fm. contours, and of banks as revealed by the 50 fm. contour; also positions of standard Irish Stations worked between 1921 and 1933.

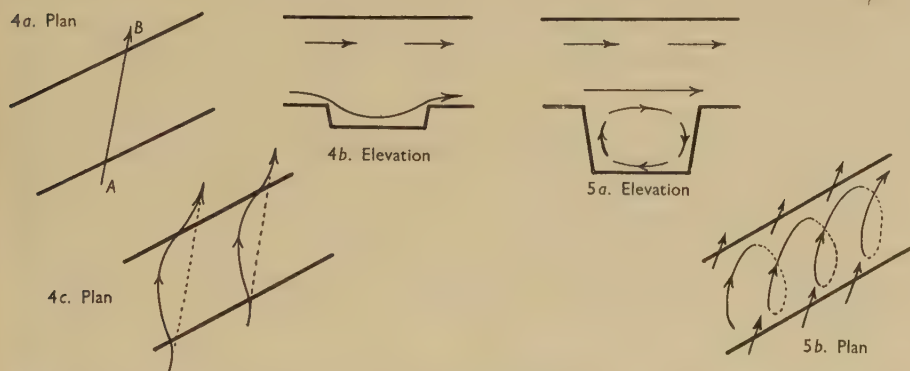
THE INFLUENCE OF BANKS AND SUBMARINE VALLEYS

It is necessary here to develop another concept needed later. Contouring the chart in the neighbourhood of the Great Sole and Cockburn Banks ($49^{\circ} 45' \text{ N.}$, $9^{\circ} 30' \text{ W.}$) reveals a very striking picture of a submarine peneplain¹ at 65 fm. (120 m.), dissected by troughs about 15-20 fm. deep like a series of submerged river valleys (Le Danois, 1938, fig. 10), the direction of which is south-west to north-east (see Fig. 3).

¹ A 'peneplain' is a gently rolling lowland produced after long-continued denudation of a land mass. The floor of the Celtic Sea conforms closely to this definition except that it is submarine. The term is graphic and more suitable than 'shelf' or 'terrace' for the arguments to be developed.

It may be remarked that the depth of 120 m. (400 ft. or 65 fm.) figures frequently in discussions of the maximum withdrawal of the sea during the Pleistocene Ice Ages (*inter alia*, Farrington, 1945; Flint, 1947).

The soundings on the charts, which are not dense enough to give any idea of the vertical sections across the troughs, do not require any gradient steeper than 1 in 100. However, it would seem that during the period of low sea-level when these troughs were probably cut, the climate was glacial and the rivers concerned drained the whole of northern France, southern and western England and Wales, eastern Ireland, and perhaps even the Clyde Basin. They should have been strongly seasonal with little flow in winter and very heavy erosive spates during the summer melting of the ice; such may well have led to deep



Figs. 4 and 5. Diagrams illustrating possible water movements above valleys or troughs dissecting a submarine peneplain. Fig. 4a, b and c: motion above shallow troughs; Fig. 5a, b: over and in deep troughs.

entrenchment between steep banks when carved in consolidated rock. However, 60 miles to the south, Bullard & Gaskell (1941) have made two seismic soundings of the sea floor. They believe that unconsolidated sediments at $48^{\circ} 54' \text{ N.}, 9^{\circ} 10' \text{ W.}$ extend to at least 1090 m., and at $48^{\circ} 45' \text{ N.}, 9^{\circ} 48' \text{ W.}$ to 2470 m. below the sea floor. In such unconsolidated sediments glacial rivers would have cut down exceedingly quickly; with the return of the sea the banks would have been destroyed and the river beds filled in just as easily. Only an echo-sounding survey can show quickly whether any steep banks now remain. It may then be possible to say how far such submarine valleys may canalize bottom currents in this area in a south-westerly-north-easterly direction and impede currents whose direction is at right angles to the axis of the valleys.

We can investigate the situation theoretically by a simplification of the factors involved. Consider a parallel-sided trough in an otherwise level submarine peneplain, and let a current set across the trough at an angle to the longitudinal axis of the trough. In diagram Fig. 4a, AB represents the direction of the current at peneplain level. Such a current may be produced by tidal

forces, density differences between adjacent masses of water, or wind. If the current be wind-produced, the direction of current at peneplain level would, according to Ekman's (1905) theory of wind drift, be different from that at the surface. However, if the current at peneplain level flows in a given direction *AB*, it is of no importance to the theory which follows whether the water above flows all in one direction or according to an Ekman spiral.

In order to continue the investigation, it appears necessary to differentiate between two possible forms of motion. If the water sinks into the trough and rises at the opposite side, as Fig. 4*b*, the theory developed by Ekman (1923, 1927, 1932), and summarized by Sverdrup (in Sverdrup, Johnson & Fleming, 1942, pp. 466-9), would seem to apply. In the Celtic Sea the influence of a shallow trough would be to cause a deviation in current direction, as shown in Fig. 4*c*, and further, would cause a stationary disturbance on the sea surface. For further details the reader is referred to the original papers of Ekman.

However, it is not at all certain that the troughs existing in the Celtic Sea may be considered as shallow, so that a different form of motion appears possible. Water at submarine peneplain level may slide over water within the trough, Fig. 5*a*, exerting a shear on it, causing it to move and ultimately to form an eddy in a vertical plane. Only when the return current sets across the trough at right angles would this eddy be cyclic; in all other cases the motion would be spiral with a transport of water to the right as in Fig. 5*b*. There would seem to be a further complication to such motion. Energy is transferred at peneplain level in much the same way as by wind acting on water; consequently, within the trough a form of Ekman spiral, much modified by turbulence, should be set up.

When conditions along the trough are not uniform, yet another possibility may arise. At a point where the current within the trough is weak, the water approaching its edge could turn back on itself at the same level, producing something akin to a 'rip current' (see Shepard, Emery & La Fond (1941) for a description of surface rip currents).

A theoretical solution at this stage seems impossible, but it appears from the survey outlined above that turbulence from bottom to surface should be great, and that energy is dissipated, causing diminution in the original currents. This turbulence may redistribute nutrients throughout the water column and, providing it is not excessive, favour their more efficient usage by plants.

Tentative inferences for the Great Sole-Cockburn Bank Area which can be substantiated only by fresh observations on the spot, are: (1) that currents, however caused, may tend to conform to the direction of the submarine valleys; (2) that in summer the thermocline should be more weakly developed than in neighbouring undissected regions of the shelf having the same depth and exposure to ocean swell; (3) that a useful stock of inorganic nutrients, including iron, may be maintained in the upper photosynthetic zone right through the

summer; and (4) that the falling off in late spring in production of phytoplankton, so characteristic of the waters near Plymouth, where the thermocline may develop very strongly, may be much less marked.

CASCADING IN THE WINTER OF 1929-30

Within the 100 fm. contour of the Celtic Sea extensive salinity and temperature observations, collected mostly between 1921 and 1933 by the Irish Fisheries Service under the direction of the late Mr G. P. Farran, are available, but for the waters bathing the continental slope there are far fewer. All the observations have been taken from the 'Rapports Atlantiques' and the 'Bulletins Hydrographiques' published annually by the International Council for the Exploration of the Sea, Copenhagen. Satisfactory proof of cascading is difficult to adduce on the basis of salinity and temperature alone and to clinch the argument the measurements of oxygen and pH made on board *Armauer Hansen* in 1914 have been invaluable.

Other factors being similar, cascading should have developed most strongly in those winters in which air temperatures were low. To assess meteorological cooling of the sea, some way of integrating departures of temperature from the mean during the whole winter is needed; not an easy task. As a lead, air temperatures in February at Valencia (Cahirciveen), Scilly and Guernsey were examined. Of the years 1921-33, 1930 was the coldest at Valencia (below average by $2.7^{\circ}\text{C}.$) and at Scilly (by $2.3^{\circ}\text{C}.$); Guernsey was somewhat cold but only below average by $1.3^{\circ}\text{C}.$ By contrast in 1929, whereas Valencia and Scilly were average, the Guernsey mean February temperature was $2.7^{\circ}\text{C}.$ below average. This was reflected in the discrepancy in temperature difference between the Hurd Deep, north-east of Guernsey, and the waters south-west of Ireland (Cooper, in Steven, 1949, Appendix). In 1924, and again in 1932, the whole area was below average by $0.9-1.2^{\circ}$ and $1.4^{\circ}\text{C}.$ respectively. The year 1927 was average, whilst 1926 and 1928 were well above average, and consequently unattractive for our present purpose.

On this evidence the winter of 1930 appeared most likely to yield results. In mid-February of that year the density, σ_t , of bottom water in the northern Celtic Sea along the meridian of $8^{\circ}\text{W}.$ was around 27.3 and along that of $9^{\circ}\text{W}.$ 27.4. West of Co. Mayo, 200 miles to the north and 3 months earlier, H.M.S. *Ormonde* had found that water having σ_t 27.3-27.4 lay between depths of 400 and 700 m. (Fig. 6). If one may correlate observations made so far apart, it would seem that the shelf water in the northern Celtic Sea was heavy enough to sink over the slope to between 400 and 700 m. Unfortunately, there is yet another consideration which makes it unwise to base the theory of cascading on events in 1930.

Wind must always be a force, often a very powerful force, able to initiate and maintain currents. If in any winter the distribution and power of winds were such as to set up a current system in the same sense as that demanded by

cascading, then evidence from that winter ought not to be adduced in favour of cascading. For 21 out of the 28 days of February 1930, winds blew from the north-eastern quadrant and on 16 of those days the force exceeded three on the Beaufort scale. Such winds would, of themselves, provide a likely explanation of currents towards the west and south-west. This issue is discussed again later.

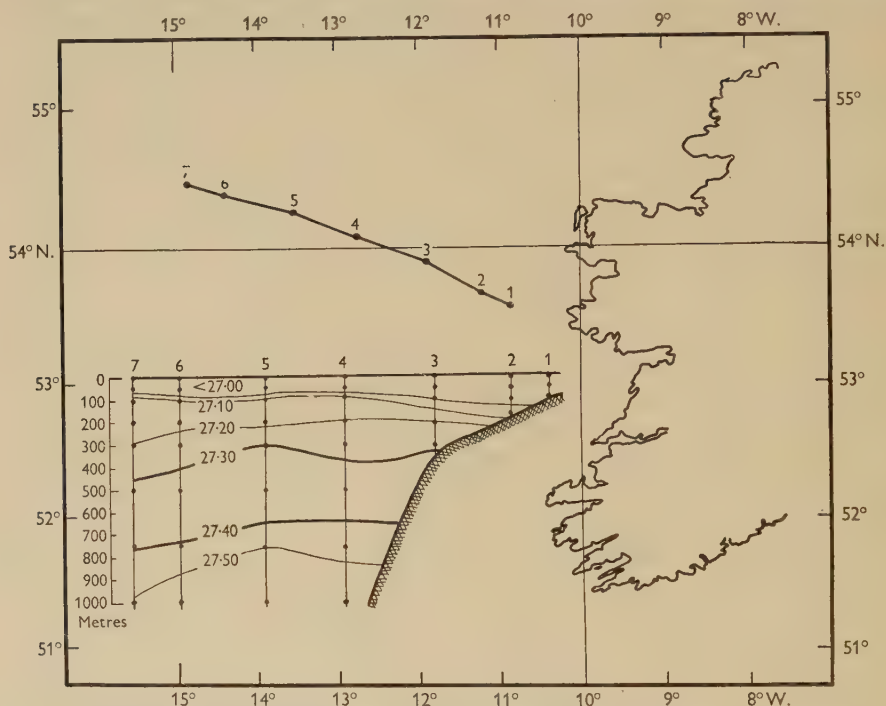


Fig. 6. Densities (shown in inset) along a section worked by H.M.S. *Ormonde* off the west coast of Ireland, 22–25 October 1929.

CASCADING IN THE WINTER OF 1926–27

Owing to the unsuitability of the winter of 1929–30, attention was switched to that of 1926–27. In this year the February air temperature at Valencia and Scilly equalled the average for the 13 years, 1921–33. With a very full network of Irish, English and French stations all worked between 15 and 20 February 1927, a simultaneous and revealing picture of the whole shelf is possible.

Temperatures were lowest ($< 8^{\circ}\text{C.}$) in the Irish Sea and the eastern end of the English Channel, and increased to the west and south-west. Within the Celtic Sea the coldest water ($< 9^{\circ}\text{C.}$) lay over the Nymphe Bank. The conditions are, however, best understood from the distribution of surface density. In the Irish Sea the low temperature was more than outweighed by the low salinity ($34.3\text{--}34.4^{\circ}/_{\infty}$ on the Holyhead-Kingstown line). In consequence, density (σ_t) at the surface (Fig. 7) increased towards the south-west, exceeding

27.30 on the Nymphe Bank at the eighth meridian and reaching 27.40 at the ninth as in 1930.

The English Channel showed quite a different pattern, since a lane of high density (>27.30) stretched throughout its entire length from the Southern Bight of the North Sea to the Celtic Sea. North of 49° N. in the latter, the distribution of surface density well represents that of the deeper water as shown by the three vertical sections (Fig. 8) whose position is shown on Fig. 7; south of 49° N. the distribution of density was utterly different and has to be discussed later (pp. 737-9). Even so, to the north there was more than 10,000 square miles of sea with density exceeding σ_t 27.30, potentially

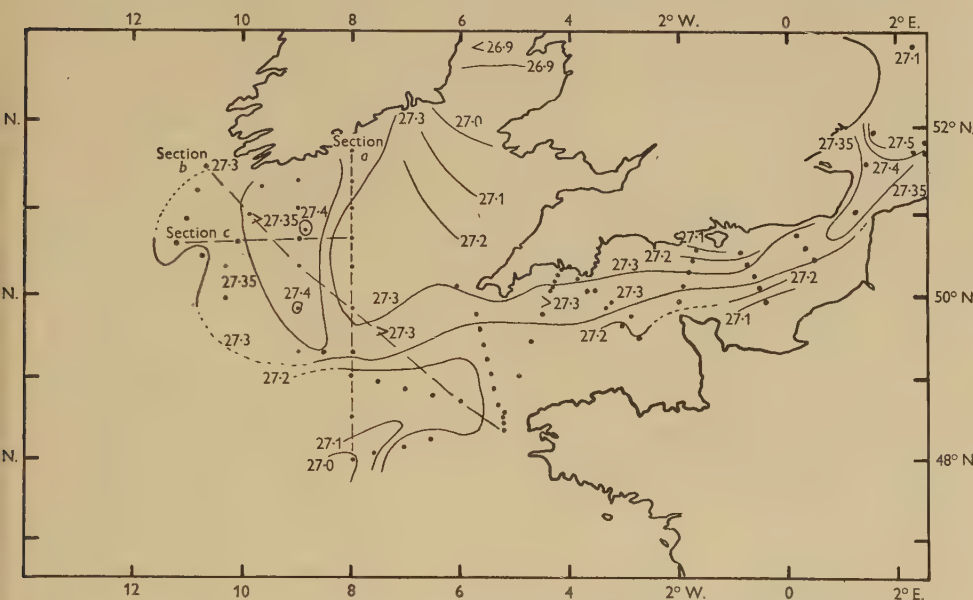


Fig. 7. Distribution of density of surface water between 15 and 20 February 1927. Also lines of three sections, vertical profiles along which are shown in Fig. 8. Profile *a* along section *a* (8° W. long.); profile *b* along section *b* (north-west to south-east); profile *c* along section *c* (approx. $50^\circ 40'$ N. lat.).

heavy enough to cascade and backed up by yet more heavy water in the English Channel.

The only observations over the edge of the slope were at the Irish station SS ($50^\circ 34'$ N., $11^\circ 17'$ W.) which was worked in August 1926 and February 1927. In August density increased downwards from σ_t 27.01 at 60 m. to 27.32 at 400 m. and 27.40 at 600 m. The ocean there was prepared to receive water of density σ_t 27.32 down to 400 m. By February such water (σ_t 27.33, 10.52 – 10.67° C., 35.59 – 35.61 ‰ salinity) had arrived between the surface and 400 m. It is the thesis of this paper that it had arrived by cascading.

This 1927 data will be used again (pp. 733-5) in an attempt to establish the course taken by cascade water.

CASCADING IN THE WINTER OF 1913-14

The evidence considered so far has shown that cascading could have happened; it has not shown that it did. The observations beyond the slope have been scanty and, in any event, assurance can never be based on salinity, temperature and density alone. The most convincing evidence was obtained by the *Armauer Hansen* in June 1914, and to make best use of it requires knowledge of conditions in the preceding winter, 1913-14. The Irish observations were few; of the usual network only stations P and Q were worked, together with several stations in the Nympe Bank area. Detailed examination of all the surface data, collected in February and March 1914, by merchant vessels in the eastern North Atlantic and Celtic Sea, has shown that some are under a heavy cloud of suspicion. The results of certain vessels, however, are consistent and appear sound, and these show that the distribution of temperature, salinity and density in the Celtic Sea in early 1914 was very similar to that in early 1927. At the Irish station P ($51^{\circ} 14' 30''$ N., $9^{\circ} 43'$ W.) and at Q ($50^{\circ} 56'$ N., $9^{\circ} 56'$ W.) the temperature, salinity and density of the water at various depths have been compared with the means which had been calculated from all the observations ever taken there in February; at both stations the 1914 values agreed almost exactly with the mean. Moreover, in February 1914, air temperatures at Scilly, Valencia and Guernsey did not differ significantly from the respective means over the 13 years, 1921-33. Both of these statements have been shown to be similarly true for 1927. Since in 1927 (Fig. 8) surface values gave a sufficient picture of conditions on the shelf down to the bottom, it is highly probable that the same was true in 1914.

In February 1914, the surface observations showed that most of the Celtic Sea away from the coasts was occupied by water having σ_t exceeding 27.30 ; a section of 120 miles along $49^{\circ} 45'$ N. latitude revealed no values of σ_t less than 27.40 . Such surface water was heavy enough to cascade, and evidently there was a great deal of it. Later two sets of observations were taken across the slope at the positions shown in Fig. 9 (sections *a* and *b*). There was an Irish line (*Bull. Hydr.*, 1913-14) at about $50^{\circ} 30'$ N. on 14 May, the densities along which are shown in Fig. 10, and a line by the *Armauer Hansen* (Helland-Hansen & Nansen, 1927) at about 48° N. on 5-6 June (Fig. 11*a*). No water heavier than $\sigma_t 27.30$ was found along either at less than 550 m., while water having density between 27.30 and 27.40 occupied the next 250 m. interval. Thus the February shelf water with the same density limits, if it had cascaded, would by May-June have sunk to some depth between 600 and 850 m. at station 6 and between 700 and 1000 m. at station 7.

For a number of years we have shown that the water of the Celtic Sea

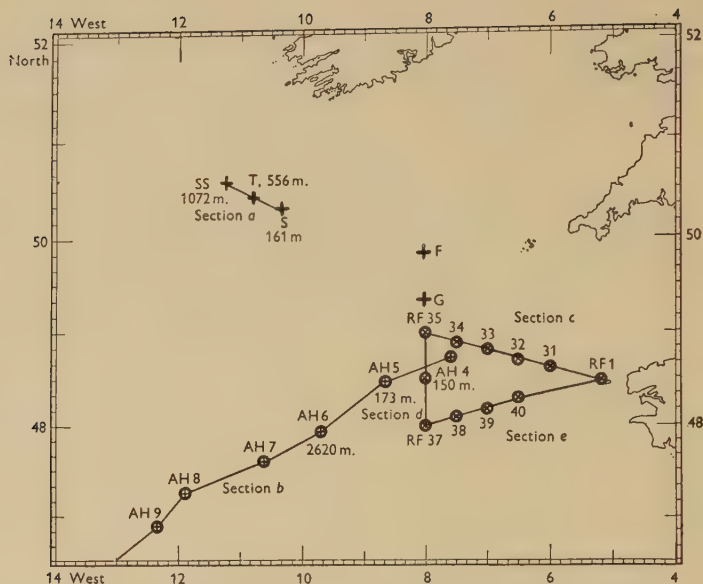


Fig. 9. Chart of sections of which vertical profiles of density σ_t are given in Figs. 10, 11 a and 13. **Section a.** Stations S-T-SS worked by the Irish Fisheries Service on 14 May 1914 (see Fig. 10). **Section b.** Stations 4-9 worked by the Norwegian research vessel *Armauer Hansen* on 5-6 June 1914 (see Fig. 11a, b and c). **Sections c, d and e.** Stations RF 1 and RF 31-40 worked round a triangle by a French gunboat on 15-16 February 1927 (see Fig. 13c, d and e).

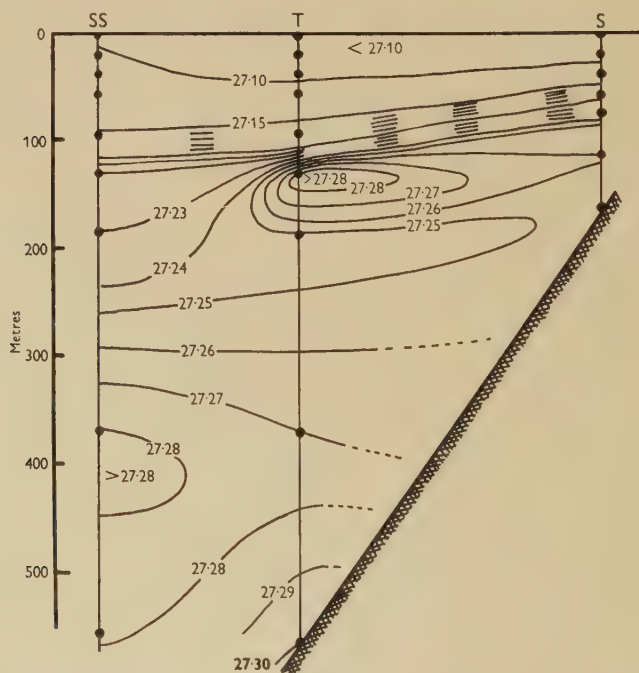


Fig. 10. Vertical profile of density on 14 May 1914, along section a in Fig. 9.

became heavy enough to cascade, but in only this one, 1914, can we show that it actually did. What is needed is some measurement to demonstrate beyond doubt that the deep water, having σ_t 27.30–27.40, had been at the surface only shortly before. The oxygen determinations made by Gaarder (1927*a*) on board *Armauer Hansen* in the first week of June 1914 achieve this (Fig. 11*b*). His stations 8 and 9 represent conditions in the open Atlantic; since in the uppermost 40 m. of water recent production by photosynthesis had exceeded consumption by respiration and breakdown, oxygen was supersaturated with respect to atmospheric pressure. From 40 m. the oxygen content decreased steadily downwards to the minimum, 67–70% saturated, in the layers between 800 and 1000 m. depth. Still farther westward this happened in North Atlantic Central water but here it occurred in water with a strong, warm, highly saline Mediterranean component. Nearer the slope in water 2620 m. deep at station 6 (47° 57' N., 9° 42' W.), as shown in Fig. 9, a very different vertical distribution was present (Fig. 11*b*). At 400, 800 and 1200 m. there were three strata of oxygen-rich water sandwiched between oxygen-depleted layers. This odd result, standing unsupported, would carry considerable doubt as to the soundness of the single oxygen determinations; but they are supported. At 800 and 1200 m. the value of pH, 8.13, was the same as at 100 m. (Gaarder, 1927*b*). Much later Buch, Harvey, Wattenberg & Gripenberg (1932) and Buch (1933) evaluated the constants of the carbonic acid system in sea water so that it is now possible to evaluate partial pressures of carbon dioxide p_{CO_2} from determinations of pH, salinity and temperature. It is necessary that pH should have been determined as described by Buch with due account of the several corrections needed. Consequently, it is unlikely that Gaarder's 1914 measurements could be suitable for accurate computations of partial pressure of carbon dioxide, p_{CO_2} , but none the less, they may be used for a rough and ready treatment sufficient for the present purpose. The results (Fig. 11*c*) are striking, since a partial pressure, $3.4\text{--}3.5 \times 10^{-4}$ atmospheres in water so deep as 800 and 1200 m. is very unlikely in water which had been unventilated for any considerable time. There seems no choice but to believe that all the water at 800 m. and most of that at 1200 m., bracketing the depleted Mediterranean tongue between, had cascaded from the shelf 3 months or so earlier. It should also be noted that the salinity at 50–200, at 800 and at 1200 m., 35.52–35.53‰, was constant; the waters agree in salinity, oxygen percentage saturation, pH and partial pressure of CO_2 and differ only in temperature and density. There can be little doubt that they represent successive stages in the cascading of essentially the same body of shelf water as the temperature fell and rose again. At 400 m., however, since the high oxygen content, 99% saturated, was associated with pH 8.05, p_{CO_2} 4.4×10^{-4} atmosphere and salinity 35.47‰, no firm conclusion may be drawn.

Water cascading down the slope should inevitably acquire considerable momentum; if, therefore, heavy shelf water should have sunk to a level of

density equal to its own, it might perhaps spread out at that level giving rise to lateral mixing along surfaces of equal σ_t . Such mixing takes place with minimum change in potential energy, the momentum or kinetic energy being used to overcome internal friction or to displace other bodies of water. If the cascade on the slope should become canalized within a submarine canyon, it would become a core which might possibly penetrate at its appropriate σ_t level many miles into the ocean. This may have been the origin of the oxygen-rich water, apparently a core, found on 7 June 1914, at *Armauer Hansen* station 10 ($46^\circ 26' \text{ N.}, 13^\circ 14' \text{ W.}$) at 600 m. (94.5% saturated) and at station 11 ($46^\circ 00' \text{ N.}, 14^\circ 03' \text{ W.}$) at 800 m. (86% saturated). These stations were respectively 190 and 220 miles from the nearest part of the slope. Moreover, their densities were no greater than 27.26 and 27.28, and the temperatures and salinities were typical of western Celtic Sea water in January or April.

THE COURSE OF THE CASCADE

In general, the water near the slope has a higher salinity than that to the east at 9° W. , at 8° W. , and over the Nymphe Bank. When cascading happens it must necessarily draw colder but less saline water towards the west or south-west, so that during late winter and early spring, a decrease in salinity should mark the course of the water cascading from the Nymphe Bank.

In 1927, fortunately, the Irish records were unusually complete, not only in February, but also in May, so that in that year it is possible to assess the changes in salinity over a wide area and so to chart the most probable course of the northern part of the cascade current. The two cruises were run between 17 and 20 February and between 6 and 10 May; in Fig. 12 the stations worked on both are shown. It will be seen that the fall in salinity was especially marked on the eighth meridian between the coast and $51^\circ 00' \text{ N.}$, at all stations worked on the ninth meridian, and at $51^\circ 15' \text{ N.}, 9^\circ 43' \text{ W.}$ This is precisely the distribution that the theory of cascading demands. It would seem that water cascading from the region of the Nymphe Bank set west-south-west across the eighth meridian between the Labadie Bank and the coast of Co. Cork. Towards the ninth meridian it would seem to have divided; the northern branch hugged the coast and passed Mizen Head in a lane 20 miles wide, whilst the southern branch set south-west or south-south-west, with its axis crossing the ninth meridian at about $50^\circ 20' \text{ N.}$ and heading towards the Great Sole Bank area. It is suspected that its further course was controlled by the bottom configuration of that much dissected region, but direct observations are lacking. A similar fall in salinity took place in other, but not in all, years.

In the 11 weeks elapsing between the two 1927 cruises, the isohalines had advanced about 50 miles to the west or south-west. This gives an average speed of the cascading water at 9° W. of about 0.6 miles per day.

A submarine bank in the way of the cascade should impede it, a submarine valley should encourage it; consequently, the fall in salinity between February and May 1927 should have been least over a bank and greatest over a valley. This was the case: on the ninth meridian at station 9C, on the edge of a bank, the fall in salinity was less by 0.03‰ ; and at station 9D, at the head of a valley, it was greater by 0.02‰ than a smoothed curve along the meridian

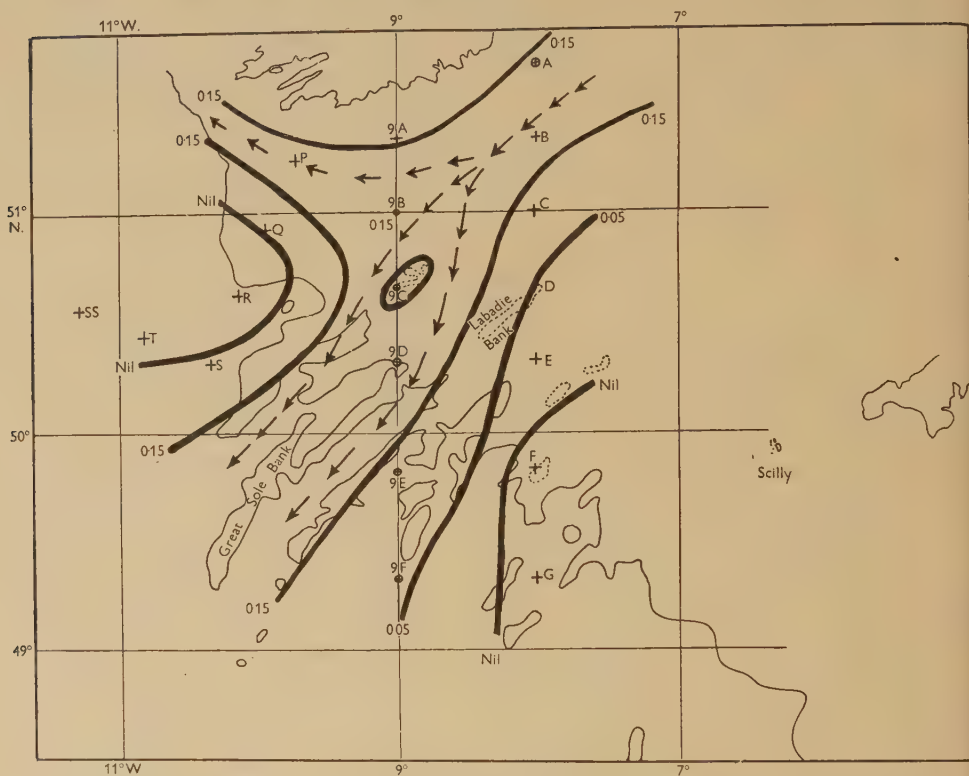


Fig. 12. Probable course in 1927 of cascading water over the shelf as indicated by the fall in salinity between 17–20 February and 6–10 May. The iso-lines represent decreases in salinity of 0.15 , 0.05 and 0.00‰ . The fall in salinity in the neighbourhood of the bank at Station 9C, shown enclosed on the chart, was 0.13‰ . The arrows show the most probable courses of the cascading water.

would have suggested. A similar deficiency of about 0.04‰ shows up on the eighth meridian at station D at one end of the Labadie Bank. These results, slender though they are, combined with the considerations set out on pp. 722–4, have assisted in the extrapolation of Fig. 12 towards the Great Sole Bank.

It is not easy to assess the effect of the Corioli force, due to the earth's rotation, upon the cascade. It operates not on residuals, but on the currents which actually flow and include relatively large alternating tidal components. One can

say only that the effect of the earth's rotation should be to encourage the cascade to hug the Irish coast and this the northern branch seemed to do.

Water from south-east of the Labadie Bank may also have contributed materially to the cascade. Since it was warmer but more saline, its course cannot be followed by these devices.

COMPENSATION WATER

The theory of cascading requires that loss of heavy water over the slope shall be made good by an inflow somewhere or other. Five sources of such compensation water may be considered:

- (a) From the north-eastern Atlantic via the North Channel and the Irish Sea.
- (b) From the North Sea via the Straits of Dover.
- (c) By upwelling at a restricted part of the slope of the Celtic Sea.
- (d) By an influx of saline but relatively warm and light Atlantic oceanic surface water.
- (e) By an influx of coastal water from the French Biscayan shores.

(a) According to Proudman (1946, p. 591) the mean current through the Irish Sea is from south to north, entering through the St George's Channel and leaving through the North Channel. In February 1927, water having density (σ_t) 26.7 lay right across the Irish Sea from Holyhead to Kingstown, so that then the Irish Sea could have made no contribution to the cascade. It is unlikely that it ever does.

(b) The flow of water through the Straits of Dover has been very fully investigated at the Varne Lightvessel by Carruthers (1935). The mean flow of water in the nine Februaries of 1927-35 was 1.9 sea miles per lunar day towards N. 1° W. true. In all other months the flow was directed to between N. 14° E. and N. 33° E., whilst the strength ranged from 2.6 to 4.1 miles per lunar day. In February there is evidently strong westing and diminution of the 'normal' flow. Although this is precisely the effect which one would expect cascading from the Celtic Sea to have on the Straits of Dover current at the Varne, little confidence can be placed in the correlation. Following winds play a large part in impelling water towards the north-east through the Straits of Dover, and it so happens that February has been the month with least favourable winds. Again, March, which should be a month of strong cascading in the Celtic Sea, shows a set of average strength (3.0 miles per lunar day). Possibly more revealing is the average direction of the current, arranged in Table I, according to direction, by months for the 8 years, June 1926-May 1934.

Apart from September, which is irregular, the months with a set between N. 9° W. and N. 18° E. were those when some measure of cascading might have been expected, those with a set between N. 22° E. and N. 35° E. were months when cascading should not have occurred.

TABLE I

AVERAGE DIRECTION OF CURRENT AT THE VARNE LIGHTVESSEL, STRAITS OF DOVER, ARRANGED BY MONTHS, FOR THE 8 YEARS, JUNE 1926 TO MAY 1934

February	N. 9° W.	July	N. 22° E.	October	N. 26° E.
May	N. 11° E.	August	N. 22° E.	December	N. 26° E.
September	N. 13° E.			January	N. 34° E.
April	N. 15° E.			November	N. 35° E.
June	N. 17° E.				
March	N. 18° E.				

One is entitled to ask whether the backing of the current by 43° between January at the end of the Table and February at the beginning is brought about in some measure by initiation of cascading from the Celtic Sea.

This possibility is supported by the distribution of density between 14 and 20 February 1927 (Fig. 7); for then a continuous line of water heavy enough to cascade ($\sigma_t > 27.30$) connected the Southern Bight through the English Channel with the Celtic Sea. Some compensation water for the Celtic Sea cascade could have been recruited along this lane.

A coincidence which may not have been due to chance should be noted. In his first report on current measurements at the Varne Lightvessel, Carruthers (1928) discussed at length the strongest set of the current towards the French coast, as assessed between 24 June 1926 and 8 January 1928. This set of 6.1 miles per day towards S. 81° E. occurred between 16 and 19 February 1927 during light local winds. Although not a reversal of the current it was a marked departure from normal. It would seem to reflect the pulse of the Celtic Sea cascade, transmitted along the Channel and revealed at the Varne in the absence of the currents, due to prevailing winds, which often completely obscure it.

Again, the strongest south-westerly set, 12.9 miles per day towards S. 51° W., reported in Carruthers's second paper (1935), occurred in the cold winter of 1930—on 7–10 February—when we have reason to believe that the Celtic Sea cascade was very strongly developed (pp. 743–4).

It is, therefore, possible that cascading from the Celtic Sea in February and March may provide one, but only one, of the forces which control currents in the Straits of Dover. Its effect may be to oppose, but seldom to cancel, the forces which tend most often to drive water from the Channel into the Southern Bight. The amount of compensation water from this source is probably small.

(c) Strong persistent easterly or north-easterly winds, blowing surface water from the shelf over the ocean, should here create the situation recognized the world over as favourable to upwelling of deeper nutrient-rich ocean water from several hundred metres. In winter such winds are cold winds which also favour cascading. Much of the slope west of the Celtic Sea should then be blanketed with a poorly stratified water which has recently cascaded. Upwelling of this, even if it should happen, would merely restore the *status quo*.

It is suspected but not proved (Cooper, 1947) that internal waves in stratified

deep oceanic water approaching the slope may run up it like a surface wave up a beach, so introducing nutrient-rich waters to higher levels. If a weakly stratified blanket of cascaded water lies between the stratified ocean water and the slope, the energy of the waves should be absorbed by the blanket and fail to reach the slope. Upwelling due to internal waves should therefore occur, never in winter and early spring, but perhaps in summer and autumn. Simultaneous cascading and upwelling seem to be incompatible. Unless very definite evidence can be found, it would seem that compensation, by upwelling, of water lost by cascading is very unlikely.

(*d* and *e*) It would seem, therefore, that the main compensation for water lost by cascading should be provided by surface oceanic or Biscayan water entering the Celtic Sea from the south-west. Such intrusion of oceanic water frequently occurs and has been called by Le Danois (1938, p. 150) in French a 'transgression' and in English an 'expansion'. He defines a transgression as '*un mouvement périodique, d'amplitude variée, des eaux atlantiques d'origine tropicale, déterminant un empiètement momentané de ces eaux sur les eaux d'origine polaire et sur les eaux continentales. Les eaux de la masse transgressive ont toujours une salinité supérieure à 35‰*'. This concept has been strongly attacked by von Schubert (1935), although it may apply on occasion. None the less, on the theory here presented, in February and March cascading provides the primary driving force in the circulation of the Celtic Sea and the intrusion of Biscayan or oceanic water is the necessary consequence.

The inflow of very warm and saline (14°C. , 35.43‰ salinity) water in mid-February 1927 at about 48°N. , 8°W. has already been described by Le Danois (1929), who hailed it as '*un phénomène de transgression très net et d'une grande intensité*'. He figured the distribution of salinity and temperature but not that of density. Unfortunately, the French observations of temperature reported in the 'Bulletin Atlantique' for 1927 scarcely meet modern requirements, since they were printed either as whole numbers, e.g. 10° , or to one decimal place which was never a cypher. Statistical examination suggests that they may not be accurate to better than $\pm 0.3^{\circ}\text{C.}$ equivalent to an uncertainty in σ_t of about ± 0.05 . This numerical uncertainty, combined with the apparently fantastic distribution of density which they revealed, has led to their being regarded with reserve. Now they dovetail with the other data here considered to give a credible but still remarkable account. It is unfortunate that the cliff-like break in density occurred in the narrow zone between the Irish and the French observations and could have been produced by a systematic error in either. The Irish records through the years include some evident misprints, but otherwise very extensive work on them has left little doubt as to their essential accuracy. The French records, as has been said, have not inspired confidence. It is of importance, therefore, that surface densities at three positions near Ushant worked by three different ships within five days are concordant. Consequently, it is not unreasonable to accept the whole of the French

observations of temperature in 1927 within the limits of accuracy suggested above.

Date	Vessel	Position	Temperature (° C.)	Salinity (‰)	Density (σ_t)
16. ii. 27	<i>Salpa</i> (M.B.A., Plymouth)	E3 48° 34' N., 5° 13' W.	10.05	35.39	27.27
16. ii. 27	French gunboat	RF1 48° 30' N., 5° 13' W.	9.5	35.28	27.27
11. ii. 27	Liverpool-Charente steamer	48° 27' N., 5° 13' W.	10.1	35.37	27.24

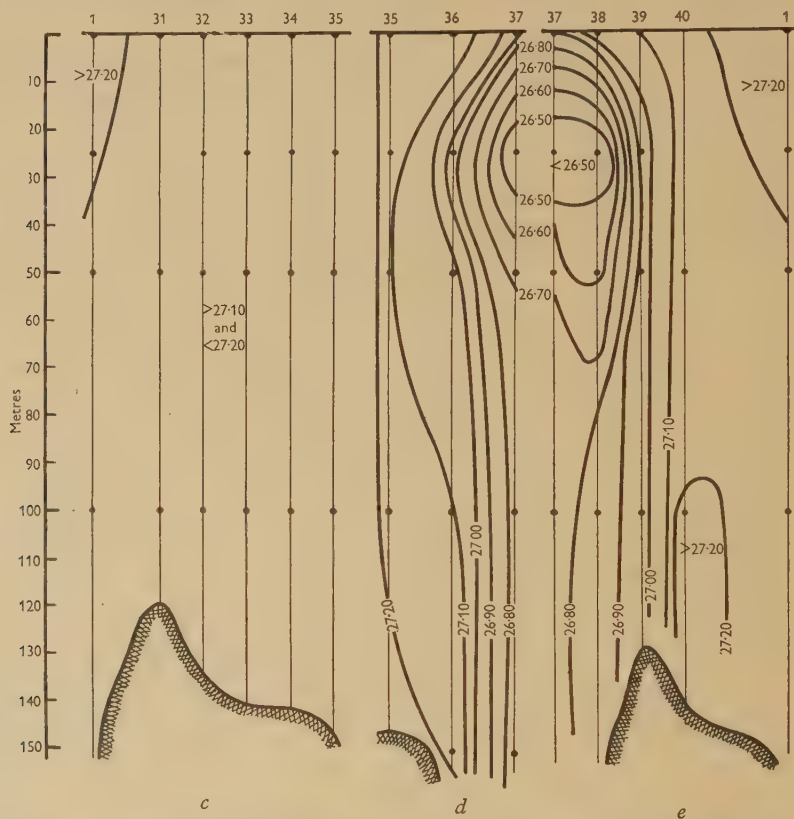


Fig. 13. Three vertical sections of density, *c*, *d*, and *e*, forming a triangle west of Ushant worked by a French gunboat on 15-16 February 1927. Positions are given in Fig. 9. Section *d*, Stations 35-37 also forms part of Fig. 8*a*.

Three vertical sections (Fig. 13), one along the eighth meridian between 48 and 49° N. and the other two completing a triangle to a point near Ushant (as shown on Fig. 9), illustrate the nature of the intrusion: an invaginated core or current about 30 miles wide and about 50 metres thick, sheathed on all sides by denser water. The most spectacular feature was the overlay or apron of surface water 0.5 σ_t -unit heavier than the water at 25 m. Considered as a problem in statics, such a distribution was impossible, for it should have been

destroyed by vertical mixing in a very short time. It could have persisted only in a strongly dynamic system; the core of water of density (σ_t) 26.5, driving east-north-east through the position 48°N. , $7^\circ 45' \text{W.}$ must have been moving very fast towards the 30-mile-wide gap between the Shamrock Knoll and Parson's Bank. This seems to be another example of how bottom configuration may control currents.

At first sight the overlay of colder water having density 27.0 might seem to have arrived on the scene as a rapid surface drift driven over the main current by northerly or north-easterly winds. This could not have happened since the Daily Weather Reports show that no such winds blew. Alternatively, one may ask whether surface cooling of the warm intrusion could have been brought about quicker than the cooled water could be carried downwards. The air temperature over the northern Celtic Sea, taken as the mean of all observations between 6 February (0100 hr.) and 14 February (1800 hr.) at Valencia, Roches Point (Cork Harbour), St Ann's Head (Pembroke) and Scilly was 6.3°C. To the southward, air temperatures are in general higher, but on that occasion they were unlikely to have been so; although temperatures over inland Britain were much lower than over the Celtic Sea, those over the whole of France were lower still, being continuously below freezing-point from 8 to 13 February (Synoptic Charts to Daily Weather Reports). Winds blowing from the south-east over France should have been even colder than those from the north-east over Great Britain.

The entering oceanic water, warmer than 14°C. , was therefore exposed to air at least 8°C. colder, a situation inevitably leading to warming of the air and surface cooling of the water. The warming of the cold continental air as it passed over the Celtic Sea shows up very clearly on the synoptic charts. The open question is: could isohaline water 2.5°C. colder, due to rapid atmospheric surface cooling, and more than $0.5\sigma_t$ -unit heavier than the water beneath have persisted long enough to be observed? Even when wide allowance is made for the nature of the observations, there remains little doubt that it did. If this is accepted, then the core of warm light water at 25–50 m., to have remained recognizable, would need to have moved very fast indeed. So far, there has been no opportunity to clothe this qualitative model in quantitative dress.

It is suggested that the invaginated current or core of warm water had been sucked in at a point of weakness over the slope, as into a void, to compensate water lost from the shelf by cascading. Such a compensation current may be expected on occasion to be narrow, fast and well defined. By contrast, a 'transgression' due to forces at work in the open ocean, and pressing warm water into the Celtic Sea against the inertia of the water already there would seem likely to create not such a core but rather a phalanx of water advancing slowly and relentlessly on a wide front.

On this occasion the balance of evidence is considered to lie heavily against a 'transgression' due to oceanic causes and in favour of a compensation

current, called into existence and demanded by earlier and simultaneous cascading south-west of Ireland.

Productivity of the Celtic Sea and English Channel will be much affected by whether this oceanic or Biscayan water, entering to compensate the cascaded shelf water, has a greater, similar, or less content of nutrients. There are no nutrient analyses of Atlantic surface water at midwinter when the total stock may be assessed. At mid-January 1947 in the English Channel north of Brittany an extensive patch of warm (11.5°C), saline ($35.39\text{--}35.46\text{‰}$) water was found, which had evidently entered recently either from Biscayan coastal regions or from the Atlantic to the south-west. Its phosphate content was very low, $0.38\text{--}0.40\text{ mg.-atom/m.}^3$, less than two-thirds of that in the Celtic Sea at the same time. Although this may not have been compensation water in the sense considered here, none the less, it may indicate the nature of the change in nutrient balance which cascading brings about. The result suggests one line which future investigation should take.

CASCADING ELSEWHERE

The principle of cascading, i.e. winter cooling over relatively shallow banks or shelves in temperate latitudes to form water heavier than that in the neighbouring ocean at a greater depth, may apply widely. The Celtic Sea faces the Atlantic Ocean to the south and west, and is bordered by land and the shallow-lying Irish Sea to the north, and by the Bristol and English Channels to the east; its exposure to the continental slope and the ocean has a strong southerly component. In the northern and north-easterly parts of the Sea, water in winter will be most strongly cooled because it is shallower and always it will tend to be colder because it is farther from the equator than the water to the south. The two effects reinforce one another, so that cascading is favoured. In general, it is in border seas facing the equator that cascading is most likely to develop strongly.

In a sea, such as the North Sea, which faces towards the Pole, the two effects oppose one another so that cascading is much less likely to develop. Off the Atlantic Coast of North America the cold, low-salinity Labrador current introduces a complicating factor of great magnitude. In the neighbourhood of the Falkland Islands results obtained by the *Meteor* (Wattenberg, 1933, and other relevant *Meteor* reports), in no way conflict with extensive cascading occurring there, but no definite conclusions can be drawn. At first view, the shelf around the Cape of Good Hope seemed a likely place for cascading, in spite of its poleward exposure, but examination of the *Meteor* and *Discovery* Station Lists shows that cascading does not take place; the inflow of the warm water in the Agulhas and Benguela currents far more than compensates winter cooling. The writers know of no other data for seas bordering the Atlantic where cascading might occur. In the eastern basin of the Mediterranean,

Nielsen (1912, p. 142) recognized that the temperature of the deep water is determined by the inflow of colder masses of water from the Aegean Sea, and the Adriatic. This is nothing but a statement of cascading from two seas which face the equator.

A POSSIBLE APRON OF SURFACE WATER BEYOND THE SLOPE RICH IN ZOOPLANKTON

Let us reconsider Fig. 2. As the water moves from A to B it should carry with it its content of plankton. Furthermore, when at C it cascades over the slope those plankton organisms, lacking the power to swim, should be carried down. Neritic species should be found in the cascade water, perhaps at a considerable distance from the slope. It should be possible from amongst them to establish biological indicators by means of which cascade water may be recognized.

Plankton animals able to swim, especially those which undertake diurnal vertical migrations towards the surface, would swim up from the cascade into the overlying apron of warmer more oceanic water. In general, this apron would not be moving in the direction of the cascade away from the shelf, so that the cascade may be considered as flowing under it. Animals and plants unable to leave the cascade will be carried on and down; vertical migrants, whilst in the apron above, will not. Vertical migration should therefore tend to concentrate the more vigorous zooplankton from the cascade into a narrow stationary zone in the more oceanic water which would not normally provide their habitat and in which they might not be expected.

A characteristic of this zooplankton community should be the high proportion of vigorous shelf species known to undertake vertical migrations, and the scarcity amounting, perhaps, to complete absence, of shelf zooplankton with only weak powers of swimming and of shelf phytoplankton which should remain in the cascaded water.

In the absence of cascading, plant food will be available in quantity only in the illuminated layers; in contrast, cascading over the slope should each day carry down below the illuminated zone a supply of plants and of the herbivores which have recently fed. This supply may be replenished each day. The vertical range within which vertical migrants can find relatively rich food supplies should therefore be extended during cascading into the region between, say, the 100 and 200 fm. contours. Such conditions may favour the production of zooplankton of the kind which the 2 m. stramin ring net catches. Moreover, these concentrations of zooplankton are likely to be sought out by pelagic fish.

The above picture should apply where the cascade flows over a smooth slope. If, however, the slope should be dissected by strongly developed submarine valleys or canyons, an even more strongly differentiated distribution

might result. If such a valley should cut back into the shelf, it would seem that it could act as a gutter into which the heavy cooled water might tend to collect. Sample models should show whether this conception is, in fact, physically sound. If the gradient of the floor of the valleys should be steeper than that of the shelf, the rate of descent of the cascade should be accelerated, resulting in a concentration of vigorous zooplankton in a restricted zone above the valley at the expense of neighbouring undissected sections of the slope. The richest regions of all in winter may therefore lie above submarine valleys or 'canyons' in the slope where such exist.

The economic conclusion from this line of reasoning is that in the apron of more oceanic water overlying the cascade above the edge of the continental slope, pelagic fish are likely to find concentrations of food organisms greater than anything to be found on the continental shelf. They may provide a rich drift net fishery for vessels able to stand up to the weather.

The whole of this picture applies only when cascading is proceeding strongly, say in February and March, and not then in every year. It is suspected that in those months cascading provides one of the dominant driving forces of the water circulation in the whole of the Celtic Sea, and may have a powerful effect on the life patterns and rhythms of all animals living there. With the cessation of cascading, this concentration of planktonic food organisms and pelagic fish should tend to break up.

THE TRANSPORT OF IRON

Other investigations (Cooper, 1948) have shown that the stock of iron in the sea water of the Celtic Sea tends to become concentrated in particles suspended in the bottom-most layers. A cascading bottom current of the type described here should have a powerful tendency to strip the stock of iron from the Celtic Sea, and to carry it over the slope into the ocean abyss from which much of it may never return. Although soluble nutrients may be made good by upwelling somewhere at some season or other, it is not easy to see how the stock of iron, mostly particulate, can be replaced in this way. Indeed, there may be no cycle of iron unless a geological time scale is used; plants and animals over the shelf may have to rest content with a supply of iron on slow but steady one-way passage from rivers to the ocean bed.

REDISTRIBUTION OF NUTRIENTS

Nutrients carried over the slope in cascading water would be lost from the shelf. Lack of balance between loss and replenishment may underlie the large variations in the nutrient resources in the English Channel in different years.

It may be profitable to discuss the likely fate of nutrients in the Celtic Sea at the end of this cascading period. As the surface waters warm up in spring

they will become too light to cascade, although the underlying unheated water would continue able to do so. A marked redistribution of the waters would then start, and should have a number of consequences.

One result of the vernal phytoplankton outburst is an increase in the amount of faeces and detrital matter containing nutrient elements. These particles tend to sink into deeper water, leading to an enrichment of this with nutrients at the expense of the upper illuminated layers, a cumulative process. When this happens in an enclosed area, the autumn overturn restores the original situation and, in the course of the year, there is no loss. But when this deeper, enriched water is moving towards the west or south-west under the influence of the cascade while the warmed surface water is relatively stationary, a redistribution of nutrients should come about. The deeper water would be carrying away a rich store of nutrients of which some would spill over the slope whilst some, at the end of cascading, should come to rest as a rich reservoir towards the edge of the shelf.

The surface water in the eastern and north-eastern area of the Celtic Sea would have been depleted. If, in that area, the water which compensates the lost deep water has an equal nutrient content, by the autumn the position will become restored. If, however, as the slender evidence would suggest, the compensation water is poorer in nutrients, an overall impoverishment in the eastern area will result. Whatever the effect may prove to be, it should be most marked in those years in which cascading of bottom water persists particularly late, say, into May. Near the slope a high concentration of nutrients would naturally always be attributed to upwelling; however, at the season when cascading is coming to an end, a high nutrient content there might equally well have resulted from redistribution on the shelf beneath the discontinuity layer. The two situations should be distinguishable by the distribution of density along sections from the shelf over the slope to the deep ocean. Upwelling should not occur when the distribution of density strongly favours cascading.

SOME APPLICATIONS

In 1927, the stage was set for cascading to occur, but only in 1914 has it been possible to show beyond question that it did. This was due to the measurements of oxygen content and of pH made by Gaarder on board *Armauer Hansen*. In future studies of slope oceanography in this area, determinations of oxygen will be essential, for with their help bodies of water with similar salinities but very different histories may be distinguished.

Although in 1930 conditions were very favourable for cascading, owing to the north-easterly and easterly winds, the evidence was not presented on behalf of the theory of cascading. Now that that theory has been tested in other years, a debating point must be made. The strong cooling in the winter of 1930, reinforced by favourable winds, should have driven an abnormally

large amount of water off the shelf. This water would have had to have been replaced somewhere within the Celtic Sea by an abnormally large influx of some other water. About 9 months later in the English Channel near Plymouth the change-over occurred in the nature of the sea water which has had such far-reaching consequences. All we can now do is to note the coincidence; whether they were cause and effect we cannot yet say.

How often cascading occurs we do not know. The winter of 1948-49 has been exceptionally mild, the mildest since 1921. Fortunately, it was possible to work two stations on the eighth meridian on 9-10 March 1949, which have given a good idea of cascading potential then (Table II). The cascading

TABLE II

Position		Temperature (°C.)	Salinity (‰)	Density (σ_t)
50° 36' N., 8° 04' W.	Near Station D on Labadie Bank	9.97-10.00	35.23-35.24	27.15-27.17
49° 50' N., 8° 00' W.	Station F	10.28	35.22-35.23	27.09-27.10
50° 03' N., 5° 43' W.	Longships bearing 3.5 miles 355°	9.58-9.65	35.21-35.23	27.19-27.22

potential of Celtic Sea water having density (σ_t) around 27.15 is probably slight; there have been years in which it has been even less. It is clear that the tendency of Celtic Sea water to cascade, and for consequent incursion of Atlantic surface water in compensation, will vary greatly from year to year. Although it provides a theme fraught with possibilities in studies of the biological productivity of the whole area, its further examination has had to be deferred. So far, stress has been placed on cascading of shelf water to considerable depths over the slope, but it should be clear that at the beginning and end of the cascade the water of intermediate density will flow off only as a shallow sub-surface flood. Consequently, when cascading has occurred, water which has acquired 'neritic' or coastal characteristics whilst on the shelf should stretch out into the Atlantic beyond the slope for many miles, with consequent effects on the character of the plankton living there.

Since an ultimate aim is to correlate the physical oceanography of the Celtic Sea with the distribution of plants and animals, attention should be drawn—for what it is worth, which may prove to be little—to a notable resemblance of the diagrams showing the probable course of the cascade in 1927 as deduced from the fall in salinity (Fig. 12) to Steven's diagram (1948, p. 525, fig. 5) illustrating the migrations of the mackerel at this season. In both diagrams there are bifurcating arrows south of the Irish coast about 8°-8° 30' W., the one suggesting cold relatively brackish water drawn towards the cascades over the slope, the other mackerel migration routes.

THE EFFECT UPON FISHERIES IN SHALLOW WATERS OF
AUTUMN COOLING OVER BANKS

As a rider to the general thesis of this paper let us now consider a shallow flat-topped submarine bank rising from a considerable depth on all sides (Fig. 14). From the basic argument (p. 721), in cold weather a shallow bank of limited extent would seem always to be the site of convergence and descent, never of divergence and ascent.

The local divergences and convergences studied by Woodcock (1944) and others, were not the result of bottom topography and are quite different from the phenomenon here to be described.

On such a declivity plant cells are likely to be carried below the photosynthetic zone before they can have had time to divide and multiply. Phytoplankton should be sparse. None the less plankton, plant and animal, should be sucked into the convergence from a distance and then carried down the slope of the bank.

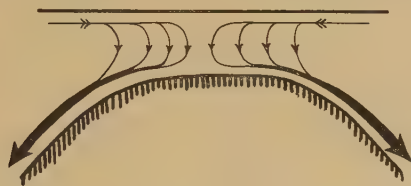


Fig. 14. Local cascading over a bank on a shelf

On such a declivity, demersal fish and filter-feeding sessile organisms should continuously be presented with a fresh supply of food. Such animals may tend to congregate on declivities in cold weather rather more than they do in warm. Again, there are animals which undertake the arduous process of reproduction in autumn and winter when the supply of food in the sea is sparse; is there any evidence that such animals seek declivities where they are exposed to cascading water?

This local form of cascading may arise during cold weather at any season of the year, but it should develop most strongly during the autumn when the rate of cooling of the water is at its greatest. Only then is it likely to occur on a scale sufficient to compete with the forces opposing its development, viz. wind drift, waves and tides.

One of the declivities where mackerel congregate in November and December is the Voyageur Bank in the Straits of Dover (Steven, 1949). Nearby lies the Varne Lightvessel from which very large numbers of surface hydrographical observations have been made. Those for the autumns of the 4 years, 1935-38, have been examined. During October and November the average rate of cooling was about 0.07°C . per day rising during December to 0.10°C . per day; after Christmas, further cooling took place much more slowly and sporadically.

Since the higher the temperature the greater the effect of a fall of 1°C. upon increase in density (Atkins, 1925) the rates of increase in density in November and in December were about the same. Moreover, local cascading should have developed just as strongly in October. If, therefore, local cascading is the magnet which draws mackerel to the declivity in November and December, it ought to do so during October also.

Falls in temperature of the water at the Varne of more than 1°C. in 4 days, accompanied by increases in density (σ_t) of more than 0.15 are as set out in Table III.

TABLE III. OCCASIONS AT THE VARNE LIGHTVESSEL IN THE FOUR SEASONS (OCTOBER-MARCH) OF 1935-36 TO 1938-39, WHEN TEMPERATURE FELL BY MORE THAN 1°C. IN 4 DAYS AND DENSITY INCREASED BY MORE THAN 0.15 σ_t UNIT.

Date	Fall in temperature ($^{\circ}\text{C.}$)	Increase in density (σ_t)	Fall in air temperature at 01.00 hr. at Lypne ($^{\circ}\text{C.}$)
5-9 Nov. 1938	1.1	+0.21	See text
13-17 Nov. 1936	1.8	+0.33	7.9
13-17 Nov. 1937	1.0	+0.17	5
1-5 Dec. 1936	1.0	+0.24	6.5
9-13 Dec. 1935	1.3	See text	See text
17-21 Dec. 1938	2.3	+0.44	15.5
21-25 Dec. 1938	2.1	+0.25	
25-29 Dec. 1937	2.3	+0.20	8.3

The air temperatures at the near-by meteorological station at Lypne at 01.00 hr. for each period have been extracted from the Daily Weather Report. In early November 1938, it is clear that local air temperatures had little to do with the fall in sea temperature which must have been associated with horizontal currents. The period 9-13 December 1935, has to be considered as part of the longer period, 1-13 December, during which the air temperature at Lypne at 01.00 hr. was $6-11^{\circ}\text{C.}$, colder than that of the sea at the Varne which was falling rapidly. Density increased by 0.33 σ_t -unit over the whole period, but air and sea temperatures and density do not correspond in detail. On the other occasions a sharp fall in the temperature of the air accompanied that of the sea, and leaves no doubt that the one was the cause of the other. Local cascading should have been much favoured on these occasions. Most favourable of all should have been 14 and 15 November 1936; 13, 14 and 15 November 1937; 1 and 2 December 1936; 2-13 December 1935; 18-26 December 1938; and 25 and 26 December 1937. If records are extant to show that landings of mackerel from the Voyageur Bank area were well above average on these occasions, the general thesis would be very strongly supported. Unfortunately, a negative result would not finally dispose of it since, if no mackerel were present in the area, they could not be caught either on declivities or anywhere else.

The autumn of 1938 differed from the other three. The rate of cooling was greatest in October and December, and slight in November. On the present hypothesis, therefore, any mackerel present in the Straits of Dover should have congregated on the Voyageur and similar Banks in October, scattered in November and reassembled in December. Since this issue is evidently of direct importance to the fisherman it merits further direct observation.

SUMMARY

In the Celtic Sea, to the south of Ireland, water in some winters becomes sufficiently cooled and heavy to flow to the edge of the continental shelf and to run down the continental slope to a depth of several hundred metres. A theory of the phenomenon, termed 'cascading', has been developed. Three winters have been examined in detail.

In February 1927 much water, heavy enough to cascade, was present in the Celtic Sea and also in the English Channel. A probable course and speed of the cascading water over the shelf has been established. Since there were few observations of salinity and temperature over or beyond the slope, and none of oxygen anywhere, the theory cannot be completely established on the basis of the 1927 observations, full though they were.

What is needed is some measurement to demonstrate beyond doubt that water, having density σ_t 27.30–27.40, had been ventilated at the surface only shortly before. The measurements of oxygen content and pH made by Gaarder on board the *Armauer Hansen* in June 1914 achieve this. The distribution of density on the shelf in the previous winter has been pieced together. There remains little doubt that water off the slope at 800 and 1200 m. depth had cascaded shortly before. Direct observations, designed for the purpose, are now needed to clinch the argument.

Loss of water from the Celtic Sea by cascading requires that somewhere or other compensation water must enter. The Irish Sea appears to contribute neither to the cascade nor to the compensation water. The cascade may reduce the strength of the current through the Straits of Dover towards the North Sea, but seems seldom able to annul it. Little compensation water would seem to come that way. Since simultaneous cascading and upwelling over the slope seem incompatible, the only considerable sources of compensation water would seem to be the surface waters of the Atlantic Ocean and Bay of Biscay. A very strong inflow from the Atlantic into the southern Celtic Sea in February 1927, previously considered to be a 'transgression', is here regarded as compensation water, the necessary consequence of cascading.

The inflow consisted of an invaginated core of warm, saline water sheathed on all sides by heavier water. The surface water was heavier by 0.5 σ_t -unit than the water at 25 m. The meteorological and dynamic meaning of this odd, very unstable distribution has been discussed.

Although the tendency to cascade was strong in February 1930, events in that year have not been adduced as evidence for cascading. Strong north-easterly and easterly winds could have driven water off the shelf without help from cascading. Winds and tendency to cascade, together, should none the less have brought about great loss of water from the northern Celtic Sea, and made necessary a large inflow of compensation water somewhere or other. Attention is drawn to the coincidence of this with changes in the nutrient salt regime in the western English Channel a few months later.

It is considered that the submarine banks and valleys of the Celtic Sea are likely to exert considerable control over the direction taken by currents initiated by cascading or by winds. A final conclusion demands more knowledge of bottom configuration and of the currents which actually flow, particularly in winter.

Theoretical argument suggests that during strong cascading an unusually high concentration of large vigorous carnivores may develop in the apron of more oceanic water overlying the cascade over and beyond the slope. This apron might possibly be the site of a rich pelagic fishery.

It is suggested that the stock of iron in the Celtic Sea may be on slow but steady one-way passage from rivers to the ocean bed.

Marked redistribution of nutrients may result, particularly from cascading of cold bottom water underlying surface water which has warmed up and been the site of production of plants and animals.

As a rider to the general thesis, local cascading over shallow flat-topped banks on the continental shelf during autumn cooling has been considered. Circumstances may then favour the concentration of fish over declivities.

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APPENDIX

THE NAME 'CELTIC SEA'

This paper has been concerned with the 'sea area to the south of Ireland and off the western entrance to the English Channel', a cumbersome description which defies repetition. The accounts of previous biological and hydrographical investigations in the area have suffered from the lack of any concise name, while reference to different parts of the whole has been even more difficult. The name 'Western Approaches' is incomplete, and 'Chops of the Channel' too colloquial. The area is geographically, oceanographically and biologically a unity, and it is for this reason that a new name should be justified. The need was first recognized and met by E. W. L. Holt who, at a meeting of Irish, Scottish, English and French fishery experts held at Dublin in 1921, proposed the name 'Celtic Sea', after the Celtic lands of Brittany, Cornwall, Wales and Ireland, which border it. Holt seems never to have used the name in his publications, neither is there any record of its formal adoption or of a definition. Even so, his ideas were well formulated and known, as Le Danois (1938, p. 84) testifies. The term had attained currency in French writing, as in Le Danois' book, but none in English, until Corbin (1942) used it. Since 'Celtic Sea' is so concise and self-explanatory it has been used here but is felt to need definition as follows:

The Celtic Sea covers that part of the continental shelf of the Eastern North Atlantic Ocean bounded:

- (a) On the east by the shortest line between the western point of the Island of Ushant (Ile d'Ouessant) and Lands End (Cornwall) and by the shortest line between Lands End and Ramsey Island, off St David's Head, Pembrokeshire.
- (b) On the north by the shortest line from Ramsey Island to Carnsore Point, Co. Wexford, by the south coast of Ireland from Carnsore Point to Dursey Head, Co. Kerry, and by the shortest line from Dursey Head to the 200 m. (or alternatively the 100 fm.) contour.
- (c) On the west and south-west by the 200 m. (or 100 fm.) contour.
- (d) On the south by the shortest line from the western point of Ushant to the 200 m. (or 100 fm.) line.

A BALANCE-BY-DEPTH METHOD FOR THE PHOTOELECTRIC MEASUREMENT OF THE VERTICAL EXTINCTION COEFFICIENT OF WATER

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and F. J. Warren, A.I.P.R.E.

From the Plymouth Laboratory

(Text-fig. 1)

When discussing the programme of work with Mr F. S. Russell, F.R.S., he stressed the importance of being able to make routine measurements of the clearness of the water quickly and with relatively inexpensive apparatus—something more accurate than measurements of the visibility depth of the Secchi disc. The following method is offered as a solution of this; it has several advantages; but it is naturally limited in its range as compared with the standard potentiometer method used here since 1924.

OUTLINE OF THE METHOD

It is now possible to obtain selenium rectifier cells of high sensitivity which with low-resistance galvanometers give curves relating current and light intensity that are almost straight lines up to about one milliampere. Thus if two cells give the same current in fairly bright light, in half, a quarter, or one-tenth of the intensity they will also agree. This will hold even if there is some curvature in the above relation, provided that the characteristic curves of the two cells are similar. Accordingly, connecting two such cells, positive to negative in a circuit (Fig. 1), and reducing the illumination on the more sensitive by an iris diaphragm or an opaque varnish on one of the diffusing opals mounted over each, one can use a cheap 0–50 microammeter to indicate balance. Ordinary sensitive galvanometers cannot be used at sea, and the specially balanced type developed for work at sea is expensive. The microammeter, resistance 925 ohms, is mounted as a bridge between the two circuits—as in the Campbell-Freeth method—and, since when balanced no current flows through it, its resistance is immaterial. A current does flow, however, in the cell circuit, and were there large temperature differences between the two cells some error might be occasioned. The cells are connected positive to negative, since in the reverse position, at balance, no current flows in the cell circuit and the arrangement is in effect equivalent to open circuit on a potentiometer. This

would be the best method for balance with thermopiles, but it is not so with rectifier cells, because the internal leakage then becomes relatively very important, and the cell voltages tend towards saturation in bright light.

Selenium rectifier cells are not stable, and undergo a diminution in internal resistance with age, very slow under good conditions, quite rapid when exposed to damp and high temperature. The photometer cases should contain well-dried silica gel to absorb included moisture.

It is convenient to use the more sensitive of the pair of cells for use in the sea, mounted as usual in a water-tight gun-metal or brass box, the other being mounted in a case suitable for exposure on deck. Each cell case has over its plain glass a green glass transmitting no red, and an opal-flashed diffusing glass. The uppermost should be flush with the rim so as not to cut off low-angle light. As usual the sea cell is suspended by a bridle with two wires, to which the twin-cored rubber cable is attached by a wide loop, so as not to cast

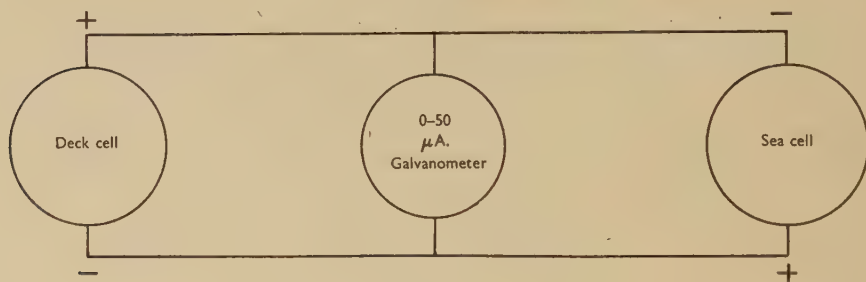


Fig. 1.

much shadow. It was possible to bring the pair of cells, as mounted, to exact equality by applying a little opaque varnish to the under side of the deck-cell opal. The deck cell was the more sensitive when mounted. Placing similar pairs of opal discs over each reduced the illumination equally, and balance was maintained right down to 6% of the initial current.

For use at sea the deck cell should be placed in gimbals.

Having equalized the cells in air an additional surface-flashed opal can be placed on the deck cell and the sea cell lowered till balance is again obtained. This depth is noted on a metre wheel. The percentage illumination at that depth then equals the percentage transmission of the opal. We cannot, however, use this reading to find the vertical extinction coefficient of the water unless we apply an uncertain correction for surface loss and reflexion error, so we must make a second balance at a greater depth with a more opaque disc on the deck photometer. The latter disc is opalized throughout.

It is, however, better to eliminate surface effects by using an opaque varnish, applied to the under-surface of the deck-cell opal, to reduce the sensitivity so that without any extra opal on the deck cell a balance can be found by lowering

the sea cell to about one metre below the surface. The ship should be stern to sun so as to cause as little shading as possible.

The sequence of operations with our apparatus is then as follows. The cells are balanced with the sea cell at say 0.9 m. below the surface. The illumination is then called 100%. A flashed opal, *A*, transmitting 61.8%, is placed on the opal of the deck cell; the sea cell is lowered to balance and depth noted. *A* is replaced by *C*, a thick solid opal transmitting (when over the deck-cell opal) 32.3%, and the depth for balance is observed. *A* is now placed over *C*, forming a combination which, when over the deck-cell opal, transmits 21.1%. Another solid opal *B* is then added; the combination *A+B+C* transmits 11.0%.

We thus have observations of the depths at which the light intensities are 61.8, 32.3, 21.1 and 11.0%, of that 0.9 m. below the surface.

The vertical extinction coefficient μ_v is obtained from

$$\mu_v = \frac{2.303}{d} (\log_{10} p_1 - \log_{10} p_2),$$

where *d* is the difference in depth, in metres, between the two points at which the percentage values of the balance depth illumination are found. This method has the advantage that instead of measuring air and under-water illuminations in quick succession and obtaining an average on which to base the ratio, the latter is obtained immediately, since changes in illumination affect both cells equally. The use of the green filter restricts the measurement to a fairly narrow band. This was used since μ_v is dependent upon wave-length and green has the greatest transmission in coastal waters. Were the filter not used there would be a fictitious alteration in μ_v with depth, as the red—and later the blue—are cut off.

Since in the above formula the values of *p* are constants for the opals and their combinations, one can obtain a factor for each, which has only to be divided by the corresponding value for *d*. Table I shows the transmissions of the opals and their combinations. These are not multiplicative, but must be determined for each. This was done using a Weston rectifier cell which gave a rectilinear relation between current and illumination up to over 4 mA. when tested with a 10 Ω galvanometer on photometer bench and by the use of opals in full daylight on the roof, using a 2 mm. red-free Schott VG9 or a Chance's very similar green glass beneath the permanent opal disc. The opals and combinations selected as most appropriate for use at sea are marked with an asterisk, also the factors which have to be used for the most suitable ranges of transmission as shown in the table, which may serve as a guide for the choice of the combinations with opals of different transmission.

With a homogeneous liquid and approximately monochromatic light the relative reduction in illumination for equal increments in depth would be equal. It would be an advantage to approximate this by the use of opals; it is also

obviously best to have a good interval between the observations. The series selected for use, namely opals A , C , $A+C$, $A+C+B$ gives reductions in illumination as follows (each calculated taking the previous illumination as 100%), A 61.8, C 52.3% (namely C transmits 32.3% or 52.3% of 61.8); similarly, for $A+C$, 65.4 and for $A+C+B$ 52.2%. The intervals are thus well spaced.

TABLE I. RELATIVE TRANSMISSIONS AND FACTORS OF DIFFERENT FILTERS AND COMBINATIONS OF FILTERS

Light filter	Transmission (%)	Interval	Factor f
Flashed opal A^*	61.8	Datum level to A level*	0.481*
Thick solid opal C^*	32.3	Datum level to C level	1.130
Thin solid opal B	31.2	Datum level to B level	1.165
$(A+C)^*$	21.1	Datum level to $(A+C)$ level	1.554
$(A+B)$	20.6	Datum level to $(A+B)$ level	1.580
$(B+C)$	16.1	Datum level to $(B+C)$ level	1.826
$(A+B+C)^*$	11.0	Datum level to $(A+B+C)$ level	2.208
		A level to C level*	0.649*
		A level to B level	0.684
		C level to $(A+C)$ level*	0.426*
		C level to $(A+B)$ level	0.450
		C level to $(B+C)$ level	0.696
		$(A+C)$ level to $(A+B+C)$ level*	0.652*
		$(A+B)$ level to $(A+B+C)$ level	0.628
		$(B+C)$ level to $(A+B+C)$ level	0.381

Notes: The vertical extinction coefficient per metre for a depth interval between two levels at which the illuminations are p_1 and p_2 % of that at datum level, respectively, is f/d , where the factor $f = 2.303 (\log_{10} p_1 - \log_{10} p_2)$.

The filters and combinations marked with asterisks give convenient intervals which would not differ very greatly in thickness in uniform water. These intervals are also marked with asterisks.

WORK AT SEA

A comparison was made between this method and our standard potentiometer method using the top cell of our cube photometer, mounted beneath similar green glass and opal. It was found necessary to reduce the sensitivity of the deck cell so that in the position of balance, without extra opal in air, the sea cell remained under water always, whether the sun were shining or not. On account of shading from the ship, the under-surface balance position is necessarily higher when the sun is obscured.

To reduce the error due to drift, final measurements were made by a quick drop to an approximately ascertained position. For the same reason a 7 lb. weight was slung below the cell, as the latter was far lighter than the cube photometer.

The method is quick, the depths of balance for the four standard opals and combinations were done twice in 10 min., and with the added weight the preliminary run and the quick drop agreed very closely.

The comparison was made at station L 4, between Plymouth and the Eddystone, in 55 m. of water. The light was very variable, which made

accurate work with the standard method rather difficult. The agreement was as close as could be expected. The standard method gave $\mu_v = 0.111$ over the depth range 5–20 m.; no balance could be obtained above 5 m. With the balance-by-depth method the range 0.5–21.0 m. gave $\mu_v = 0.108$ for the quick drop. At L 3, near Rame Head, over the same range of illumination, namely down to 11.0% of the subsurface balance point, $\mu_v = 0.123$, and near the Breakwater Light in Plymouth Sound $\mu_v = 0.310$.

We desire to express our thanks to Captain Hoodless and the crew of the R.V. *Sabella* for assistance in handling the gear at sea.

SUMMARY

Vertical extinction coefficients can be determined in water using selenium rectifier cells and colour filters. The cells are connected positive to negative with a simple 0–50 microammeter across the circuit, as in the Campbell-Freeth method. There is no deflexion when the two points of contact are brought to the same potential. This is done by lowering one cell into the sea to balance the rather less sensitive deck cell. The light reaching the latter is then reduced by the successive addition of opalized plates, to approximately 60, 30, 20 and 10%, and the sea cell is lowered further to balance at each stage. The extinctions can then be calculated by the usual formula from the known percentage transmissions and the observed depths of balance. For each plate or combination a factor may thus be obtained which when divided by the appropriate depth gives the extinction. The method is rapid in operation and the drift error can be rendered negligible. The results agree with those found by the standard potentiometer method, but the applications of the new method are necessarily more limited.

MEASUREMENTS TO DETERMINE EXTINCTION COEFFICIENTS AND TEMPERATURE GRADIENTS IN THE NORTH SEA AND ENGLISH CHANNEL

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(Text-figs. 1-13)

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This is an account of work undertaken in the yacht *Colleen* during July-September 1948, to measure extinction coefficients of the sea and to collect plankton and sea-water samples in the southern part of the North Sea and English Channel.

The results of observations at twenty-five stations in the North Sea and English Channel are recorded, with descriptions of the apparatus used. Some laboratory experiments with the apparatus are described, and some of the difficulties encountered are discussed.

ACKNOWLEDGEMENTS

The encouragement I received from the Director of the Marine Biological Association really accounted for the expedition yielding these results.

I am deeply indebted to Dr W. R. G. Atkins, F.R.S. and to Dr H. H. Poole for their help in the writing of the paper, and for many suggestions concerning the interpretation of the results.

I am also grateful to many of the staff of the Marine Biological Association for their help and interest before and after the expedition took place.

I would like to express sincere thanks to the fifteen yachtsmen from Cambridge, Oxford and London who came to sea with me at various times

throughout the summer of 1948, and whose seamanship and patience, often under distressing conditions in spite of regular doses of Hyoscine, made the measurements possible.

All the apparatus was made by Messrs H. Tinsley & Co. Ltd. and I am grateful for their co-operation in all my requests.

DESCRIPTION AND USE OF APPARATUS

The apparatus for measuring opacity consisted of two matched selenium photocells of the barrier layer type, each in a sealed box with a perspex aperture (Fig. 1). Each aperture was covered with a cellulose nitrate blue-green filter, the transmission curve of which is given in Fig. 11, p. 768. Immediately above each cell was an opal-flashed glass screen to diffuse the light. Bi-cored

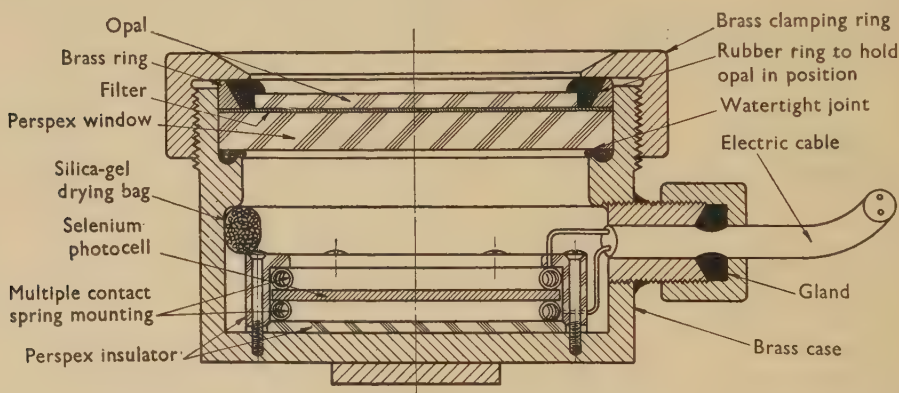


Fig. 1. Submarine photometer, in section.

rubber-covered electric cable was sealed into each box. The sea cell was suspended in a cradle (Fig. 2) to which the cable was suitably fastened for lowering. The deck cell was fixed to a wooden wedge (Fig. 2), which brought the surface of the cell horizontal when placed on the deck-house roof. The sea cell had about 30 m. of marked electric cable attached to it, and could be lowered into the sea over a pulley at the end of a 14 ft. spar which kept it clear of shadows round the ship (Fig. 2 shows a model set up).

The inboard ends of the cables from both photocells were connected to a ratiometer (Figs. 3 and 4) consisting of a $200\ \Omega$ resistance across each cell, the positive sides of each resistance were made common and a null point was found between the negative side of the sea-cell resistance and a point along the deck-cell resistance by means of a specially constructed galvanometer.¹ This null point determined the ratio of the cell currents, and hence the ratio of the cell illuminations, provided the cells had linear response curves.

¹ Full details will be published elsewhere.

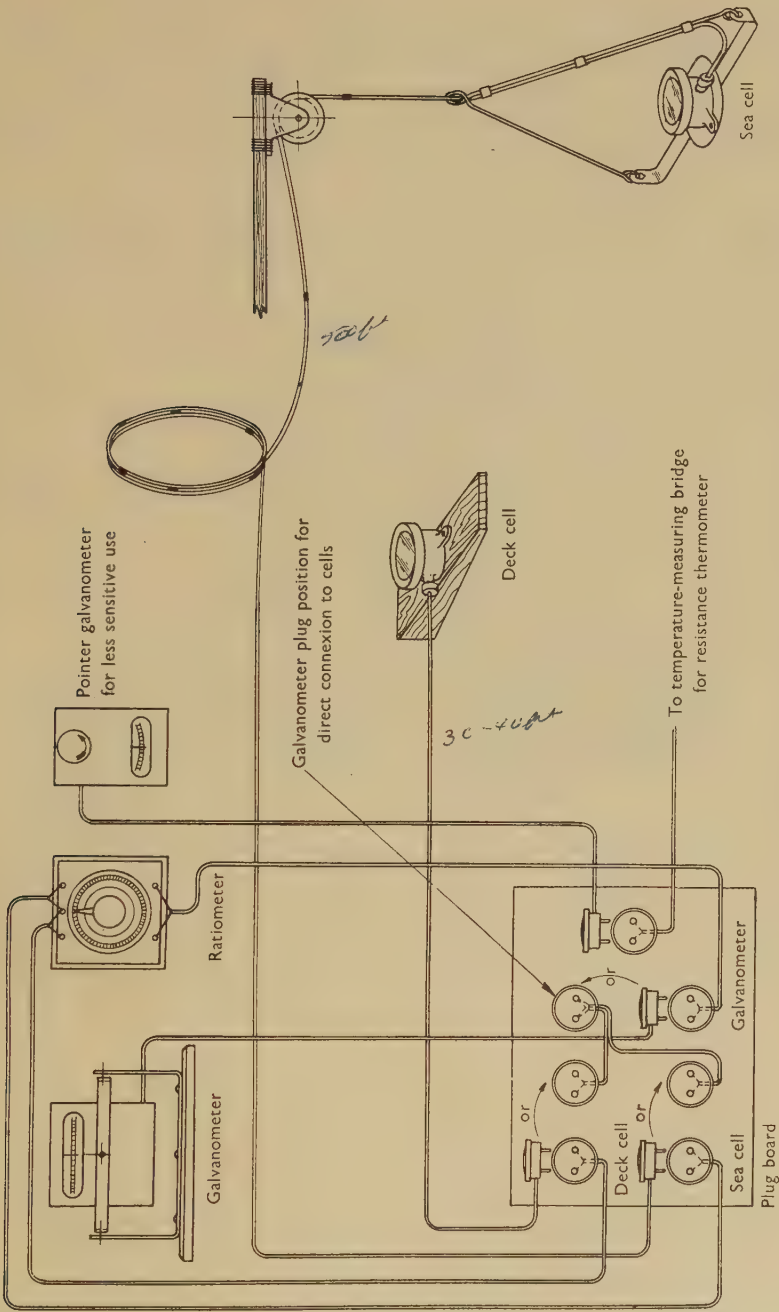


Fig. 2. Diagram of the photoelectric opacity apparatus.

According to the instructions given by the makers (the Magnetron Company), the cells give best response when the external resistance across each is between 100 and 200 Ω . There is also a temperature coefficient to be considered. But this is only serious when the external resistance is very low, so the external resistance was made as high as possible, namely 200 Ω . Experiments were carried out in the laboratory with the cells actually used at sea, to



Fig. 3. Plugboard, galvanometer and radiometer.

study their behaviour and to find over what range of light intensity the photo-electric current was indeed proportional to the intensity of the illumination. Results showed the response to be linear within 1 %, from 100 to 5 % of light intensities measured.

The photocells could also be used at sea in conjunction with filters of a known transmission ratio. One of these would be placed over the deck cell, and the sea cell lowered until such a depth was found that both cells gave the same current, the transmission ratio at this depth could then be considered the same as that of the filter placed over the deck cell. This method was used only as

a check on the ratiometer method. The apparatus consisted simply of a galvanometer placed across the cells connected in parallel. The galvanometer in this case offers the same external resistance to each cell and was $200\ \Omega$. Fig. 5 shows a circuit diagram.

The method of using the photoelectric apparatus was first to set up both the deck cell and sea cell side by side on deck in such a position that they were both free from shadows and received light from all directions. An initial reading made in this way always showed the sea cell to be slightly more sensitive than the deck cell. The sea cell was next rigged over a large pulley at

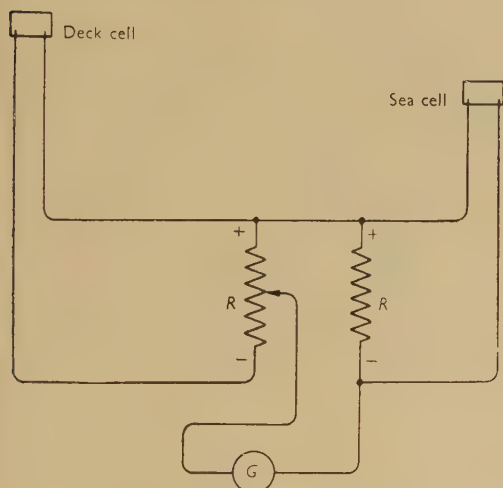


Fig. 4. Ratiometer circuit.

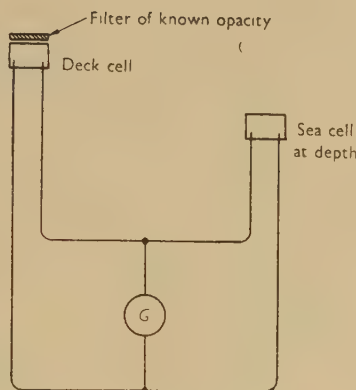


Fig. 5. Comparator circuit.

the outboard end of a 14 ft. spar placed over the ship's side in the manner shown in Fig. 2. This was always put out in a direction towards the sun, so that it was clear of any shadows under the ship.

The ratio of sea-cell current to deck-cell current was then measured, with the sea cell hanging clear of the surface and was always less than the 'on deck' ratio due to the lowering cradle being above the sea cell, thereby shielding some light off it. Finally the sea-cell was submerged to suitable depths and a series of ratiometer readings made.

The deck cell was not built on gimbals, but swung with the ship. As long as the sun was not shining, or was high enough not to cast a serious shadow from the rim of the cell across the deck cell, readings were fairly easy to make. Even when the ship was rolling considerably, the setting of the ratiometer which made the galvanometer deflexion zero could be satisfactorily determined. Violent jumping of the galvanometer spot at once told the observer down below that something was wrong with the deck cell, and that either the helmsman had let the ship's head full off so that the sun was causing shadows

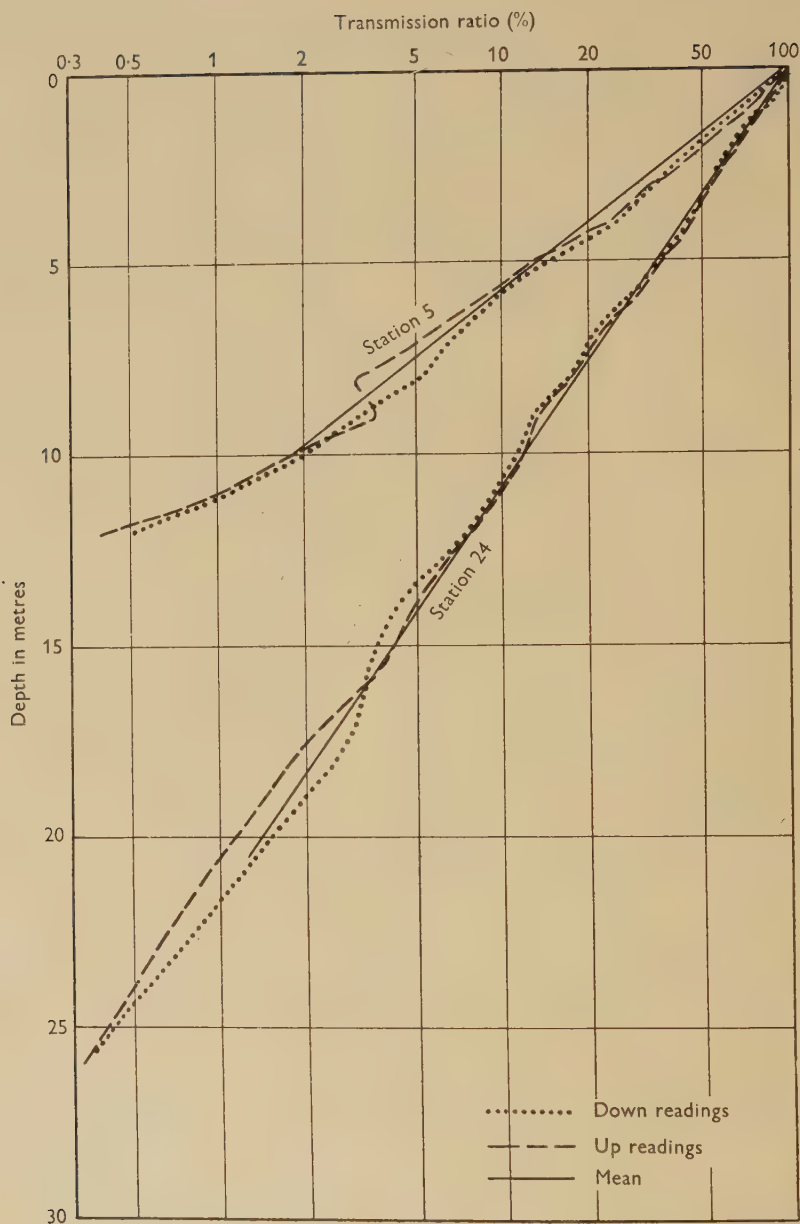


Fig. 6. Transmission ratio curves for stations 5 and 24.

from the rigging to dart across the deck cell, or that someone had carelessly walked too near the deck cell.

Even under unfavourable conditions, namely low sun and much rolling, once the sea cell was below about 10 m., the measurements became fairly easy.

In each reading the ratiometer was adjusted to make the mean deflexion of the galvanometer zero. It can be argued that more accurate results would



Fig. 7. Transmission ratio curve for station 7.

have been obtained if the adjustment had been made so that the maximum deflexion of the galvanometer had been made zero, corresponding to the maximum illumination of the deck cell as the ship rolled. The very special nature of the galvanometer used for these measurements, which had a sensitivity of 6 mm. per microampere and a periodic time of about $\frac{1}{20}$ sec., and suspended so as to operate independently of its orientation, caused it to follow these variations like an oscillograph. In practice, the results were more consistent by taking the mean position.

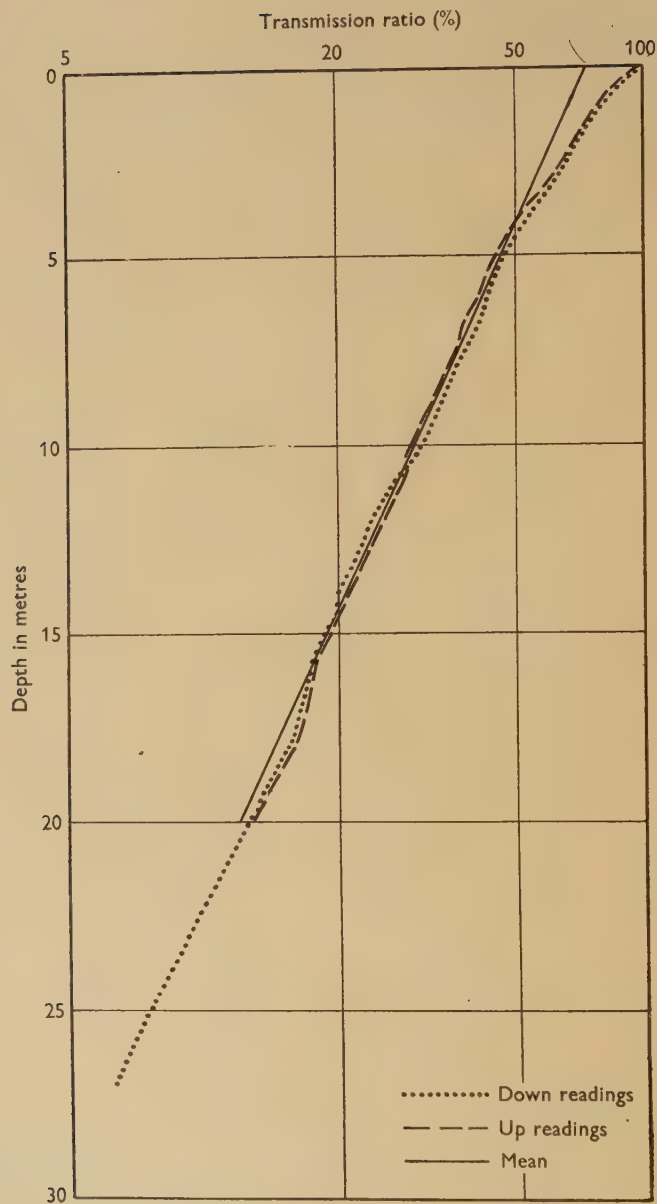


Fig. 8. Transmission ratio curve for station 8.

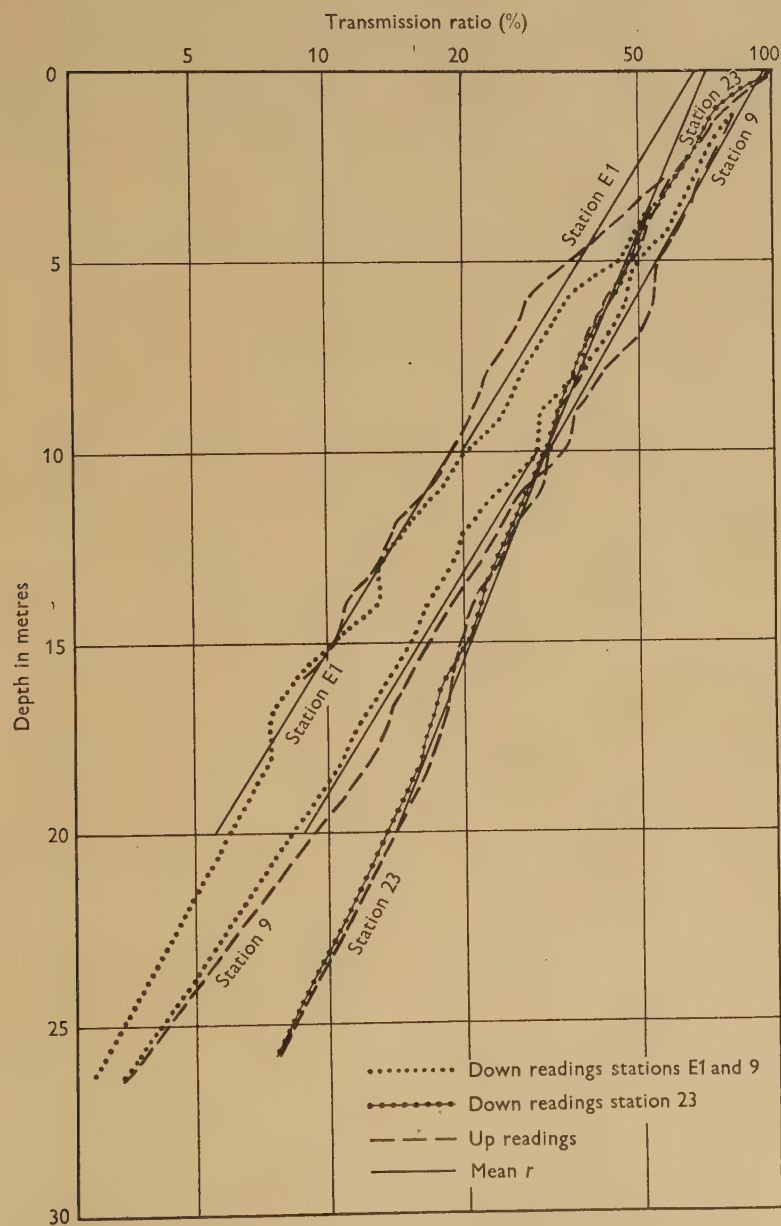


Fig. 9. Transmission ratio curves at stations E1, 9, and 23.

Readings were taken at depths of every metre down to about 18 m., and usually an additional reading at about 26 m. depth ('down readings'). As the cell was heaved in, further readings were taken at the same depths as during paying out ('up readings'), thereby giving a check on the value at each depth. Both 'down' and 'up' readings are shown in Figs. 6-10, which express graphically the results of selected stations (full results are given in Table II, p. 773).

Where a change in the slope of the graph, or, more explicitly, of the 'transmission ratio/depth' gradient, was repeated on upward and downward

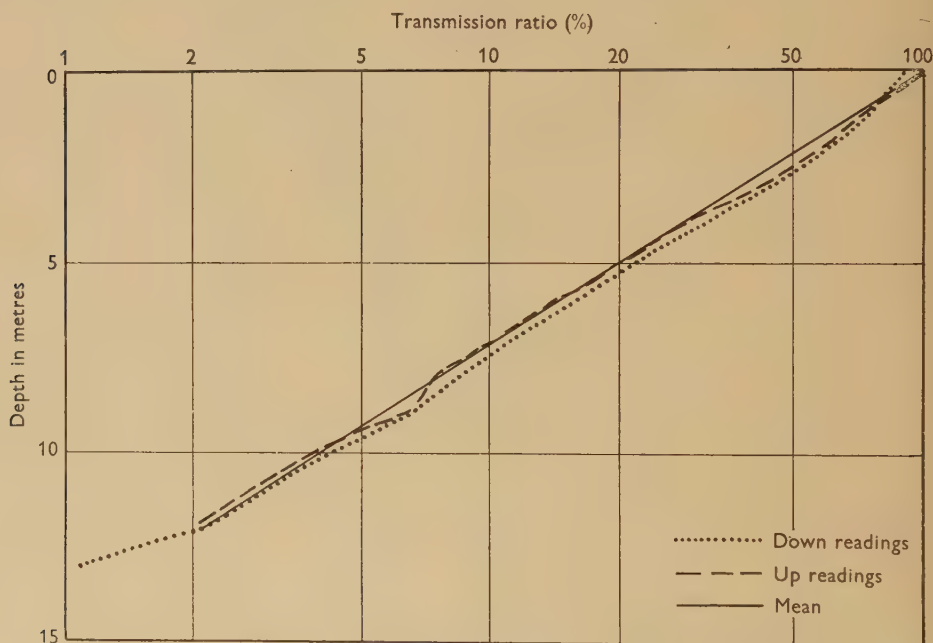


Fig. 10. Transmission ratio curve for station 12.

readings, it is reasonable to suspect some phenomena at that depth; for instance, station no. 9 at 5-6 and 9-10 m. (Fig. 9). There appear to have been layers of clearer water at that station. But if a sudden change in gradient in the 'Down readings' is not accompanied by a corresponding change in the gradient of the 'Up readings' then no definite conclusions can be drawn.

Values for extinction coefficients for 0-10 and 10-20 m. depth, given in Table II on p. 773, were derived from the mean slope of the 'up' and 'down' readings for those ranges of depth—plotted as straight lines in Figs. 6-10, in addition to the curves for the 'down' and 'up' readings. The formula used for deriving the extinction coefficient is given on p. 769.

Inconsistencies in the graphs are believed to be caused either by bad weather, when the depth of the sea cell was not always very certain, or by turbulent layers of subsurface currents which made the sea cell ride up so that its real depth was considerably less than the amount of cable paid out. The curve for station no. 7 (Fig. 7) is an example of this, particularly at 8 and 14 m. depth.

At station no. 5 (Fig. 6) there were patches of visibly opaque water drifting about, and these caused big changes in both Secchi disk readings and transmission ratio when the ship passed through one. The graph is made up of results obtained in clear patches.

Station no. E 1 (Fig. 9) is an example of bad weather results. Station no. 12 (Fig. 10) is a straightforward example of rather high opacity. Station no. 8 (Fig. 8) is an example showing possible underwater currents at 7 and 14 m. and apparently a layer of rather opaque water at the surface down to 4 m., but this may be due to the shading of the ship giving false readings near the surface. Station no. 23 (Fig. 9) is a straightforward example of low opacity but apparently showing a surface layer of high opacity, this may be due to the shading of the ship. Station no. 24 (Fig. 6) shows a good agreement between readings taken when lowering and when raising the sea cell, in spite of the water being very turbulent.

The details of other stations are left out of the text, but all the results are brought together in Table II (p. 773).

TRANSMISSION OF FILTER USED IN BOTH PHOTOMETERS

An experiment was carried out to determine the wave-length transmission curve of the filters used in the photometers. The apparatus used consisted of a spectrometer in which the field was split in two. In one half the light passed through the filter, in the other half through a sheet of polaroid. Light reached the spectrometer from a 'Pointolite' source through a collimator and a mounted Nicol's prism.

A spectrum was produced in the eyepiece by means of a diffraction grating. The intensity of the part of the field that passed through the polaroid could be controlled by the orientation of the Nicol, the intensity obeying a sine-squared law, the total extinction position being taken as zero angle.

The image seen in the eyepiece consisted of two spectra, one above the other. The bottom one being the light transmitted by the filter, the top one light transmitted by the polaroid. Having determined the extinction position of the Nicol, the cross-wires were set to different parts of the spectrum, the angle of deviation being read and the Nicol adjusted so that at the vertical cross-wire both halves of the field matched in intensity. If θ is the angle of deviation of light through the grating, then

$$\lambda = d \sin \theta,$$

where d is the line spacing of the grating and λ is the wave-length, and plotting

$d \sin \theta$ against $\sin^2 \phi$ (where ϕ is the angle of orientation of the Nicol) gives a transmission/wave-length graph.

Experimental values are given in Table I, and a smoothed curve plotted from them in Fig. 11. The position of the first sodium line was also determined, giving a check on the wave-length values.

TABLE I

Wave-length (A.)	Transmission (%)	Wave-length (A.)	Transmission (%)
4341	5.64	5199	46.89
4440	15.29	5273	32.30
4494	21.04	5360	32.35
4525	29.08	5428	16.13
4587	39.55	5539	7.54
4612	45.29	5588	4.18
4710	57.76	5636	2.37
4735	58.34	5684	1.28
4857	60.34	5747	0.58
4872	67.32	5805	0.20

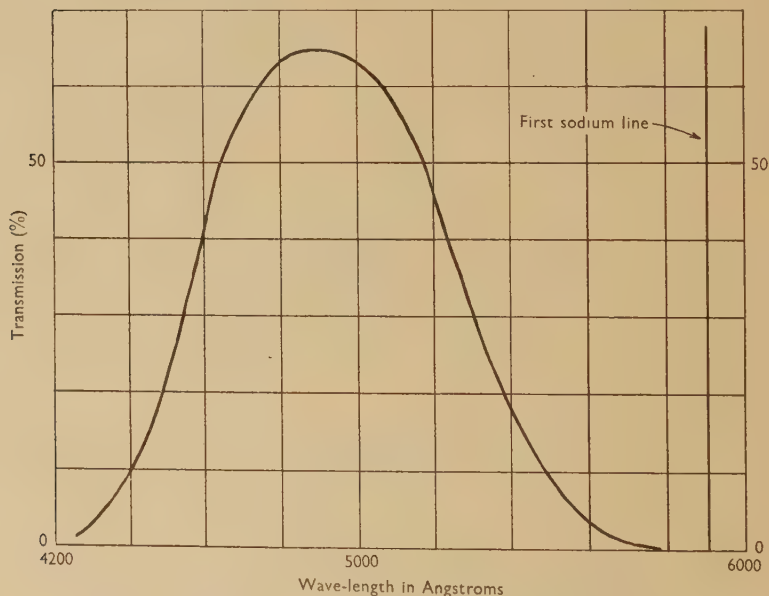


Fig. 11. Transmission ratio curve for the photometer filters.

ERRORS

The quantity measured by the radiometer has been called 'transmission ratio'. The radiometer does not measure a true ratio of light-at-depth to light-at-surface, owing to three types of error: (i) the internal and external reflexion factor (see Atkins & Poole, 1933), (ii) errors due to difference in

sensitivity of the two cells, and (iii) error due to shading of low-angle sky by the rim of the photometer. These errors are consistent, and after suitable calibration a measurement of a real ratio could be made. There are, however, two random errors for which corrections cannot easily be made: they are (i) error in estimating the depth of the sea cell, and (ii) error due to surface reflexion at the sea surface. The first of these random errors lay in not knowing the exact depth of the instrument, due to drag on its supporting cable, caused by the ship making leeway. This was only serious where the wind was force 3 or more. An efficient depth-recording instrument fitted to the submarine instrument would permit measurements to be made in winds up to force 5. The second correction is a matter of experience. The photoelectric current ratios for Secchi disk readings shown in Table III are subject to the same errors.

DETERMINATION OF EXTINCTION COEFFICIENT

Since no absolute measurements of light were made but only light ratios ascertained, there is no point in determining more than the extinction coefficient at each station, and this has been done by taking the mean gradient between 0-10 and 10-20 m. depth of the 'log transmission ratio/depth' curves for each station and using the following formula:

$$P_5 = \frac{2.3 (\log r_0 - \log r_{10})}{10}, \quad P_{15} = \frac{2.3 (\log r_{10} - \log r_{20})}{10},$$

where P_5 = extinction coefficient at 5 m. depth, P_{15} = that at 15 m. depth, r_0 = transmission ratio at surface, r_{10} = that at 10 m. and r_{20} = that at 20 m. depth.

SEA-TEMPERATURE MEASUREMENT

A resistance thermometer was used to measure the temperature of the sea at different depths. It consisted of fine platinum wire on a threaded former about 1 in. long; $\frac{1}{4}$ in. diameter enclosed in a tube. The resistance was about 100 Ω at 0° C. The tube was fixed to the end of 3-cored rubber-covered copper cable.

Compensation for the resistance of the copper cable is effected by using the 3-cored cable, and thus having an equal amount of copper resistance in opposite arms of the bridge. The third core of the cable is connected to the end of the platinum thermometer and goes to the galvanometer. By this arrangement, the copper cable is equally divided between the two arms of the bridge so that variations in its resistance with temperature are compensated. The two cores of the cable having the most equal resistance are chosen for this purpose.

The thermometer has been calibrated directly experimentally, and a table drawn up for interpolating measurements made at sea. Fig. 12 shows a

diagram of the thermometer bridge. At sea the calibration was checked at each set of readings by making a temperature measurement at the surface with a mercury thermometer.

Temperature measurements were usually made at the same time as the opacity measurements, and the nature of the temperature gradient determined down to 20 m. depth. These results are tabulated, together with the extinction coefficients. The temperature gradients were in no cases large (usually of the order of 0.02 degrees per metre) they are indicated in the last column of

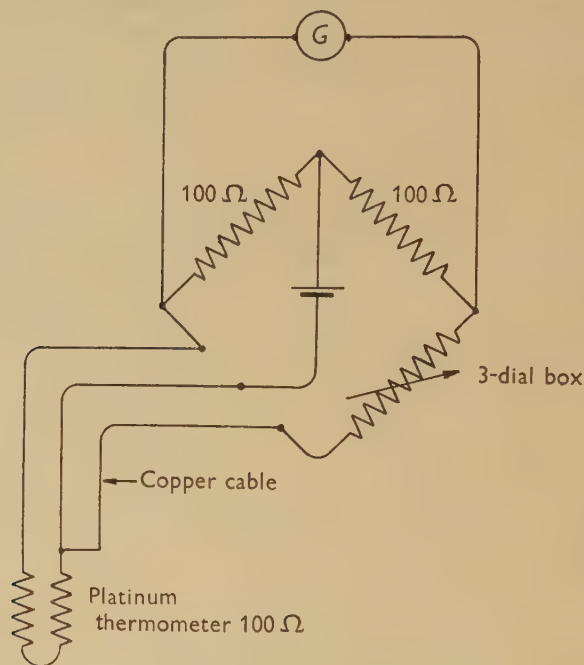


Fig. 12. Circuit of thermometer bridge.

Table II (p. 773), a plus sign means the temperature falls with depth, a negative sign means it increases with depth and a zero sign means no appreciable change.

SECCHI DISK READINGS

Readings were taken with a 12 in. Secchi disk at each station, even when weather conditions were too bad for photoelectric measurements to be made, and there are a sufficient number of contemporary Secchi disk and photoelectric readings to interpret any Secchi disk reading taken when no photoelectric reading was taken as an extinction coefficient to within certain limits of accuracy (see Table III, p. 774).

It is interesting to notice the relationship between Secchi disk readings and the transmission ratio at the depth at which the Secchi disk disappeared as measured photoelectrically.

Very roughly, the Secchi disk disappears from view at a depth where transmission ratio is approximately 20%, but from the data available (see Table III) it varies from 16.1 to 25.0%. The mean of all the values is 20.7 with a standard deviation of 3.0. By placing the readings in columns, for conditions of bright sun, no sun, rough sea and calm sea, etc., we should expect to get a smaller error for each set of conditions. Unfortunately there are not enough readings available to draw satisfactory conclusions (see Appendix II, p. 780), but the indications are as follows:

(i) In a rough sea, whether there is no sun or intermittent sun, the transmission ratio at which the Secchi disk fades out is of the order of 24.1%. (There are insufficient readings to show whether sun or no sun really makes a difference, still less to show the degree of error.)

(ii) In a calm sea, the transmission ratio at which the Secchi disk fades out is about 19.5%, possibly a little higher in bright sun than when overcast (20.4 and 18.6% are values for bright sun and no sun, but the difference is scarcely significant). The lower value for a *calm sea* as opposed to a *rough sea* is suggestive.

(iii) The standard deviation (σ) for all 'calm sea' readings is estimated as 2.7. For calm sea 'with bright sun' (seven readings) it is 2.8, and for calm sea 'with no sun' (five readings) it is 1.9. The latter conditions would be expected to be ideal, and do in fact produce more consistent readings than those in bright sun (as far as significance can be attached to the relatively low value of $\sigma = 1.9$). But the increase in consistency cannot be called very great.

A DISCUSSION OF OPACITY RESULTS

The positions of the stations and the main results from them are given in Table II, and further details from some stations respecting Secchi disk measurements are given in Table III. The course taken by the yacht can be seen on the accompanying map (Fig. 13), on which are also marked station numbers and grades of opacity of the water.

The particulars in Table II include extinction coefficients, which have been determined from measurements of the light transmission with depth and from Secchi disk readings,¹ and temperature measurements at the middle of the two depth ranges for which extinction coefficients were calculated.

From Table II it will be noticed that in the southern North Sea extinction coefficients of between 0.40 and 0.092 were obtained (except for one station

¹ A sufficient number of contemporary Secchi disk readings and photoelectric readings were made for independent Secchi disk readings, to be interpreted as extinction coefficients within sufficient accuracy for many purposes. See also above, p. 770.

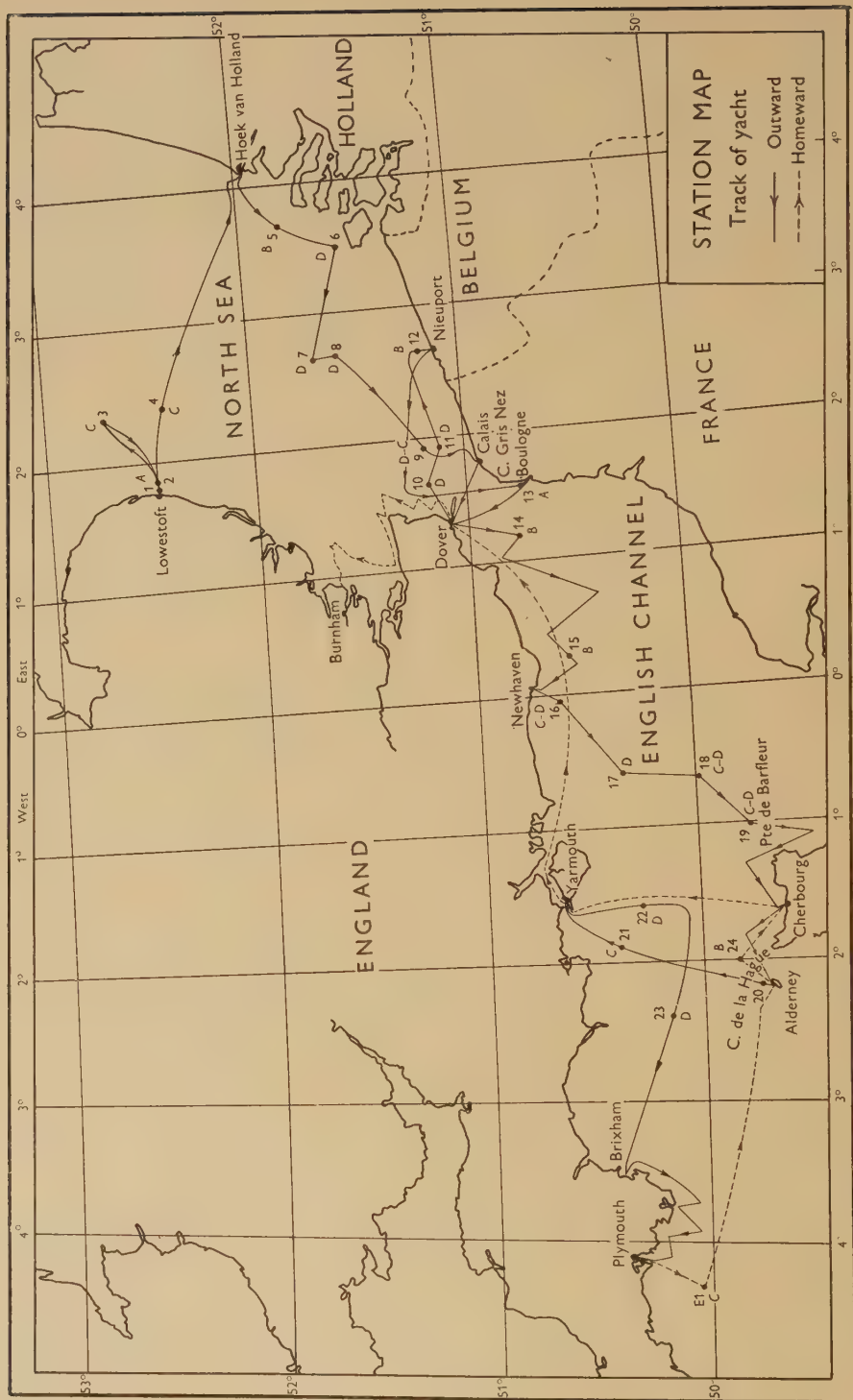


Fig. 13. Map showing the course of the yacht and the position of stations at which readings were taken.

TABLE II. POSITIONS OF STATIONS WORKED AND MAIN RESULTS OF THE LIGHT AND TEMPERATURE MEASUREMENTS

Station no.	Position	Date	Extinction coefficient		Secchi disk (m.)	Opacity	Salinity (‰)	Temperature (° C.)		
								5 m.	15 m.	Gradient
1	52° 28' 8" N., 01° 47' 5" E.	15. vii. 48	1.24	—	1½	A	33.81	14.1	—	—
2	52° 29' 4" N., 01° 52' 0" E.	15. vii. 48	—	—	3	A	—	13.0	12.9	—
3	52° 43' 8" N., 02° 18' 2" E.	16. vii. 48	0.143	0.139	12½	C	34.31	13.1	13.1	0
4	52° 26' 8" N., 02° 24' 5" E.	19. vii. 48	—	—	11	C	—	—	—	—
5	51° 51' 0" N., 03° 38' 0" E.	23. vii. 48	0.396	—	10½, 3½	B, A	32.73	13.5	13.3	—
6	51° 35' 0" N., 03° 29' 0" E.	23. vii. 48	—	—	15½-16½	D	35.07	15.0	15.0	0
7	51° 48' 5" N., 02° 38' 5" E.	24. vii. 48	0.104	0.092	13	D	35.25	14.5	14.6	—
8	51° 36' 1" N., 02° 41' 2" E.	24. vii. 48	0.088	0.092	13½	D	—	15.4	15.3	—
9	51° 12' 0" N., 01° 54' 0" E.	25. vii. 48	0.101	0.124	11½	D-C	—	16.1	16.1	0
10	51° 11' 8" N., 01° 39' 0" E.	29. vii. 48	0.097	0.097	14½	D	35.23	15.4	15.1	—
11	51° 08' 0" N., 01° 57' 0" E.	29. vii. 48	0.111	0.109	15	D	—	15.9	15.7	—
12	51° 11' 5" N., 02° 41' 5" E.	30. vii. 48	0.321	—	5½	B	—	18.0	17.9	—
13	50° 46' 2" N., 01° 34' 0" E.	5. viii. 48	—	—	3	A	—	18.2	18.0	—
14	50° 47' 0" N., 01° 12' 0" E.	10. viii. 48	0.247	—	6½	B	35.40	14.6	14.7	0
15	Beachy Head 7 miles 332° true	11. viii. 48	—	—	7	B	35.18	14.9	14.7	—
16	50° 36' 0" N., 0° 03' 2" W.	14. viii. 48	0.123	0.110	—	C-D	—	16.0	15.5	—
17	50° 21' 0" N., 0° 34' 0" W.	15. viii. 48	—	—	12	D	—	—	—	—
18	50° 0' 0" N., 0° 38' 0" W.	16. viii. 48	0.136	0.097	10	C-D	35.30	15.2	15.2	0
19	49° 45' 0" N., 01° 0' 0" W.	16. viii. 48	0.128	0.082	10	C-D	—	16.0	15.9	—
20	2 miles due North Alderney lighthouse	20. viii. 48	—	—	11½	C	—	14.7	14.5	—
21	50° 23' N., 01° 51' W.	21. viii. 48	0.136	0.137	10	C	—	15.0	14.9	—
22	50° 16' 5" N., 01° 33' W.	24. viii. 48	0.108	0.098	13½	D	—	15.2	15.2	0
23	50° 07' 5" N., 02° 21' 5" W.	24. viii. 48	0.084	0.079	13	D	—	15.1	15.1	0
E 1	50° 04' 0" N., 04° 22' 0" W.	6. ix. 48	0.123	0.122	9	C	—	—	—	—
24	49° 47' 5" N., 02° 01' 0" W.	9. ix. 48	0.215	0.208	7½	B	35.33	—	—	—

Note. The opacity of the water (seventh column of Table) has been graded as follows: A, extinction coefficient > 0.8 , Secchi disk < 4 m.; B, extinction coefficient $0.2-0.8$, Secchi disk $5-8$ m.; C, extinction coefficient $0.11-0.2$, Secchi disk $9-12$ m.; D, extinction coefficient < 0.11 , Secchi disk > 12 m. When the two depths fall into a different grade, both letters are given, that for $0-10$ m. being put first. At station No. 5 the Secchi disk reading $3\frac{1}{2}$ m. was taken in an opaque patch, other readings at this station were taken in clear water.

close inshore off Lowestoft which gave a value of 1.24); while in the English Channel values ranged between 0.24 and 0.079.

On the whole, the agreement between the 0-10 and 0-20 m. readings is close, though a difference of some 45% of the mean value was found at station no. 19. There the surface layer was the more opaque. An extreme instance of the same effect was visible at station no. 5, as mentioned already (p. 767).

On the other hand, at station no. 9, in the vicinity of the Sandetti bank, the water became decidedly more opaque below 10 m. This was presumably due to suspended matter being taken off the top of the bank, but not mixing with the upper layers. Station no. 8, in the vicinity of the Hinder Sand, also shows an inversion of the extinction coefficient with depths, but to a smaller extent than at station no. 9.

The extinction coefficients at station nos. 6-11 are surprisingly low, as these stations are in shallow water, where there are currents of the order of $2\frac{1}{2}$ knots, which would be expected to keep a great deal of matter in suspension.

TABLE III. SECCHI DISK DATA

Station no.	Date	Secchi disk reading (m.)	Photoelectric current ratio	Sea conditions	Weather conditions
1	15. vii. 48	$1\frac{1}{4}$	21.5	Calm	Intermittent sun
8	24. vii. 48	$13\frac{1}{2}$	21.5	Oily	No sun, hazy
9	25. vii. 48	$11\frac{1}{2}$	24.5	Slight swell, ruffled surface	Bright sun
10	28. vii. 48	$14\frac{1}{2}$	23.0	Very slight swell and sea calm	Bright sun (10.00 G.M.T.)
11	29. vii. 48	15	16.1	Slight swell and sea calm	Bright sun, haze (15.00 G.M.T.)
12	30. vii. 48	$5\frac{1}{2}$	18.7	Very slight sea swell	Bright sun (low), haze (07.30 G.M.T.)
14	10. viii. 48	$6\frac{3}{4}$	17.0	Slight sea and swell	No sun
18	16. viii. 48	14	17.3	Heavy swell, smooth surface	No sun, grey sky
19	16. viii. 48	10	25.0	Sea rough, swell short	Intermittent sun 5/10 cloud. Wind force 3-4
21	21. viii. 48	10	20.0	Sea calm	Intermittent sun
22	24. viii. 48	$13\frac{1}{2}$	18.0	Oily surface, moderate swell	No sun, 10/10 cloud
23	24. viii. 48	13	23.9	Small waves	Mist and drizzle
24	9. ix. 48	$7\frac{1}{4}$	19.2	Sea calm, turbulent	Bright sun
E 1	9. ix. 48	$9-8\frac{1}{2}$	23.5	Sea moderate, medium swell	Intermittent sun

Note. When the sun is shining, its altitude and relative bearing would probably affect the Secchi disk reading, but it cannot be said with certainty whether more consistent results would have been obtained if these had also been considered. However, it is safe to say that in calm weather the Secchi disk depth is greatest when there is no sun and least when the sun is shining brightly, and in rough weather the Secchi disk depth is less than in calm weather. These observations are consistent with what might be concluded from considerations of surface reflexion under the respective weather conditions.

CONCLUSIONS

The results show that it is possible to carry out opacity observations with an accuracy depending on the weather conditions. The table of Secchi disk results probably gives the best guide to the accuracy of the other opacity results. It is not possible to calculate the overall accuracy, as the random error of the depth of the instrument plays such an important part. The main feature of these results is that they show continuous sets of readings from which the extinction coefficient can be calculated, and changes in the transmission of light with depth observed down to 20 m. The quantity that has been measured by the ratiometer is not an absolute measurement of the ratio of light at depth to light at surface but is a quantity proportional to this ratio and has been called transmission ratio. The results are probably of the order of 15 % greater than the absolute ratio.

If an accurate depth-meter could be fitted to the submarine instruments, one of the largest sources of random error could be reduced and more satisfactory results obtained.

SUMMARY

During a cruise in the southern North Sea and English Channel in 1948 a series of measurements on light penetration was secured.

The apparatus used has been described, and methods of handling it discussed. A description of the experiments for determining the transmission curve of the filters used in the photometers, has been included.

Of the systematic and random errors to which the photometer measurements were liable the most serious lay in not knowing the precise depth of the sea cell.

Extinction coefficients have been determined from the gradients of logarithmic transmission-ratio/depth graphs, and the results tabulated for each station.

Temperature gradients were never large, usually of the order of 0.02 degrees per metre, the temperature usually dropping with increased depth, frequently there was no gradient at all.

An attempt has been made to correlate Secchi disk readings with extinction coefficients, as far as the data permit.

Sea-water samples from ten stations show that generally the salinity is higher in areas of low opacity, the Beachy Head vicinity being the main exception to this.

The opacity results show clearer water than might be expected at certain stations (Nos. 6, 7, 8, 10 and 11) in the southern North Sea.

REFERENCE

- ATKINS, W. R. G. & POOLE, H. H., 1933. The photo-electric measurement of the penetration of light of various wave-lengths into the sea and the physiological bearing of the results. *Phil. Trans. Roy. Soc. B*, Vol. CCXXII, pp. 129-64.

APPENDIX

I

As specimens of the raw data, the particulars of six of the stations are given herewith:

STATION No. 8

Time: 13.45 G.M.T. *Date:* 24 July 1948. *Position:* 51° 36.1' N., 02° 41.2' E.
Conditions: excellent, hazy atmosphere, no direct sunlight, oily sea, slight swell.
Secchi disk: 13½ m.

Photoelectric measurements

Depth (m.)	Transmission ratio (%)		Temperature (° C.)		
	Down	Up	Resistance	Temp. (R)	Temp. (Hg)
0	97.5	97.5	7.58	15.93	15.5
1	79.5	79.5	—	—	—
2	69.5	70.0	—	—	—
3	61.7	60.5	—	—	—
4	54.0	51.2	—	—	—
5	47.8	45.5	7.53	15.79	—
6	44.0	42.0	—	—	—
7	41.25	38.0*	—	—	—
8	37.0	35.5*	—	—	—
9	34.0	32.5	—	—	—
10	31.25	29.5	7.52	15.76	—
11	27.0	28.0	—	—	—
12	24.0	25.5	—	—	—
13	22.0	23.0	—	—	—
14	20.0	21.0*	—	—	—
15	18.8	19.2*	7.52	15.76	—
16	17.4	17.4	—	—	—
17	16.5	16.8	—	—	—
18	15.5	15.0	—	—	—
27	6.2	—	7.50	15.71	—

* Possibly turbulence.

Calculation of extinction coefficients

From graph:

$$P_5 = \frac{2.3 (\log 72 - \log 30)}{10} = 0.23 (1.875 - 1.478) = 0.0875,$$

$$P_1 = \frac{2.3 (\log 30 - \log 12)}{10} = 0.23 (1.478 - 1.080) = 0.0915.$$

MEASUREMENTS OF EXTINCTION COEFFICIENTS 777

STATION No. 9

Time: 11.00 G.M.T. Date: 25 July 1948. Position: $51^{\circ} 12' N.$, $01^{\circ} 54' E.$ Sea depth: 15 fathoms.

Conditions: very fine, bright sun, horizon hazy, light breeze, slight swell, negligible sea, wind went flat calm during photoelectric experiments, ship rolling.

Secchi disk: $11\frac{1}{2}$ m.

Photoelectric measurements

Depth (m.)	Transmission ratio (%)		Temperature ($^{\circ} C.$)	
	Down	Up	Resistance thermometer	Check (Hg) temp.
0	94	100	15.5	15.5
1	87.5	90	—	—
2	75	79.5	—	—
3	69	71	—	—
4	61	66	—	—
5	52	58	—	—
6	49	56.5	16.1	—
7	44	52.5	—	—
8	39	42.5	—	—
9	31	37.5	—	—
10	30.5	35.5	—	—
11	25	28.3	—	—
12	21	25.2	—	—
13	19.5	22.5	—	—
14	17.0	19.5	—	—
15	15.4	17.5	16.1	—
16	13.2	15.5	—	—
17	12.0	14	—	—
18	11	13	—	—
26.5	3.5	—	—	—

Note. Bright sun would be expected to fatigue deck cell and cause sea cell to appear more sensitive on upward path. Readings of opacity support this.

Extinction coefficients (calculated as above): $P_5 = 0.101$. $P_{15} = 0.124$.

STATION No. 12

Time: 07.30 G.M.T. Date: 30 July 1948. Position: $51^{\circ} 11.5' N.$, $02^{\circ} 41.5' E.$

Conditions: weather fine, bright sunlight, very hazy, horizon visibility 1 mile, wind force 1 north, very slight sea and swell.

Secchi disk: $5\frac{1}{2}$ m.

Photoelectric measurements

Depth (m.)	Transmission ratio (%)		Temperature ($^{\circ} C.$)		
	Down	Up	Resistance	Temp. (R)	Temp. (Hg)
0	91	100	8.49	18.37	18.0
1	76.5	75.0	8.48	18.35	—
2	60.0	59.0	8.47	18.32	—
3	45.0	43.5	8.47	18.32	—
4	31.5	28.0	8.47	18.32	—
5	22.0	20.0	8.46	18.29	—
6	16.0	14.5	8.46	18.29	—
7	11.5	10.5	8.45	18.27	—
8	8.5	7.5	8.45	18.27	—
9	6.5	6.5	8.45	18.27	—
10	4.34	4.04	8.45	18.27	—
11	2.94	2.80	—	—	—
12	2.13	2.02	—	—	—
13	1.08	—	8.44	18.24	—

Extinction coefficient (calculated as above): $P_5 = 0.321$.

STATION No. 23

Time: 15.45 G.M.T. *Date:* 24 August 1948. *Position:* 24 miles south of Portland Bill, 50° 07.5' N., 02° 21.5' W.

Conditions: misty, drizzle, sea ruffled, small waves, measurements easy, Galvo spot steady. *Secchi disk:* 13.0 m.

Photoelectric measurements

Depth (m.)	Transmission ratio (%)		Depth (m.)	Transmission ratio (%)	
	Down	Up		Down	Up
0	105.5	103	11	28.2	30.5
1	82	80	12	26	26.2
2	70	69	13	23.8	24
3	59.5	59	14	21.8	21.0
4	52.0	53	15	20.5	20
5	48.0	49	16	18	18.8
6	44	43.5	17	17	18
7	39	38	18	16.2	17
8	35.8	37.5	23	8.8	—
9	33	33	26	7.5	—
10	31	31			

Extinction coefficients (calculated as above)

$$P_5 = 0.0842.$$

$$P_{15} = 0.0792.$$

STATION No. E I

Time: 14.00 G.M.T. *Date:* 6 September 1948. *Position:* 50° 04' N., 04° 22' N.

Conditions: very bad, sun casting awkward shadows, too much wind, ship never stationary, continually turning and rolling.

Secchi disk: 9.0 m. before experiments; 8.5 min. after experiments, at 15.45 G.M.T.

Photocells: initial comparison on deck, 105%; cell ready to lower, 101.5; deck cell also wet, 104; deck cell dry, 101.

Photoelectric measurements

Depth (m.)	Transmission ratio (%)					
	Down	Up	Checks			
0	101	103	—	—	—	—
1	75	80	84	—	—	—
2	67	69	—	—	—	—
3	60	54.5	53.8	51	55	—
4	50	44	42.5	41	42	—
5	45.5	35.5	35.5	36	35	—
6	34.5	28	29	—	—	—
7	30.5	26.0	25.5	25	—	—
8	27.0	22.5	23.5	—	—	—
9	25.0	21.0	19.5	18	—	—
10	20.5	19.0	17.8	17	17	18.5
11	18.0	16.8	16.5	—	—	—
12	15.0	14.0	15.0	—	—	—
13	13.0	13.0	13.0	—	—	—
14	13.0	11.0	11.5	—	—	—
15	10.5	10.5	—	—	—	—
16	8.5	8.8	8.5	—	—	—
17	7.5	8.5	8.0	—	—	—
18	7.5	8.5	5.5	—	—	—
26½	3.0	—	—	—	—	—

Extinction coefficients (calculated as above)

$$P_5 = 0.1225.$$

$$P_{15} = 0.1220.$$

STATION No. 24

Time: 10.40 G.M.T. *Date:* 9 September 1948. *Position:* north-east end of race of Alderney.
 49° 47.5' N., 02° 01.0' W. drifting north-east.
Conditions: sea very turbulent, wind light, bright sun.
Secchi disk: 7½ m.

Photoelectric measurements

Depth (m.)	Transmission ratio (%)	
	Down	Up
0	97	100
1	84	82
2	63	65.5
3	52.5	52
4	45	45
5	34.5	35
6	27	28
7	20	21
8	17	17
9	12.5	13
10	11	11.5
11	9	9.8
12	7.5	7.7
13	5.5	6.0
14	4.2	4.8
15	3.5	4.17
16	3.2	3.31
17	3.0	2.37
18	2.5	1.805
26	—	0.322

Turbulence less noticeable on 'up' path. Turbulence most noticeable at 4 and 5 m.

Extinction coefficients (calculated as above)

$$P_5 = 0.215. \quad P_{16} = 0.208.$$

II

The transmission ratio at depths at which the Secchi disk disappears under different weather conditions.

Readings were extracted from Table II as follows:

Bright sun and rough sea

Station no.	Transmission ratio*
19	c. 25.0
E1	c. 23.5
Mean = 24.3	

Bright sun and calm sea

Station no.	Transmission ratio*	Deviation*
1	c. 21.5	c. +1.1
9	c. 24.5	+3.1
10	23.0	+2.6
11	16.1	-4.3
12	18.7	-1.7
21	20.0	-0.4
24	19.2	-1.2
Mean = 20.43		—
$\sigma = 2.83$		$\sigma_m = 1.07$

No sun and rough sea

Station no.	Transmission ratio*
E1	23.5
23	23.9
19	25.0

No sun and calm sea

Station no.	Transmission ratio*	Deviation*
8	21.5	c. +2.7
18	17.3	-1.5
14	17.0	-1.8
21	20.0	+1.2
22	18.0	-0.8
Mean = 18.8		—
$\sigma = 1.92$		$\sigma_m = 0.86$

All 'rough sea' stations

(19, 23, E1)

Mean 24.1 ($\pm$ c. 1.7)

σ —

All 'calm sea' stations

(1, 8, 9, 10, 11, 12, 14, 18, 21, 22, 24)

Mean 19.7 $\pm$ 0.80

σ 2.66

* Current ratio at Secchi disk depth.

NOTES ON PLYMOUTH MYSIDACEA

By Olive S. Tattersall

Whilst working recently at the Plymouth Marine Laboratory¹ I was, very kindly, given the opportunity of examining the mysids captured during a night cruise carried out by Mr P. G. Corbin around the Eddystone Lighthouse on 26/27 August 1936.

Eight 30 min. standard oblique hauls were taken with a 2-metre stramin ring trawl, at stations situated in a circle around the lighthouse, starting 2 miles due north-east at 8.17 p.m. The second haul was taken 2 miles due east and so on, passing from station to station in a clockwise direction, the last haul being taken due north at 4 a.m. The weather was fine and clear, with a clear half-moon which set at 15 min. past midnight.

The collection included nine species, only four of which—*Anchialina agilis*, *Leptomysis gracilis*, *Gastrosaccus normani* and *Schistomysis ornata*—were present in any numbers, whilst the other five were represented by only a few isolated individuals.

Adult mysids in the open ocean live by day, for the most part, either on the bottom or swimming about in the lowest levels of the water just clear of the bottom. It has been shown by many workers (e.g. Russell, 1925, 1927, 1928, 1931; Tattersall, 1936, 1938; Fage, 1933) that many species of mysids perform regular migrations to higher levels during hours of darkness, and sometimes actually reach the surface. Shortly before dawn they begin to move downward again, and by daylight all but immature animals have regained their habitat at the bottom. In addition to this nightly upward movement, many mysids become markedly planktonic during their breeding season, and in many species the females rise to the surface to release the young. These juvenile animals remain pelagic but gradually seek deeper water as they approach maturity (Fage, 1932, 1933; Tattersall, 1938).

In oblique hauls such as were used on the Eddystone cruise, it is not possible to say at which levels the animals were mainly taken, but certain points arise which bear out the observations of earlier workers. The first haul was taken before daylight had completely faded and the upward migration had not yet begun, for only five specimens were taken. At 9.14 p.m., when the second haul was taken, 458 mysids were captured, of which more than half were immature. Hauls 3 and 4 showed a steady increase in numbers but, for some reason, the numbers in hauls 5 and 6 fell considerably, rising again sharply in hauls 7 and 8.

The hauls are analysed in Table I. Hauls 4 to 8 were sub-sampled, one-tenth being counted.

¹ I should like to express my gratitude to the Director, Mr F. S. Russell, F.R.S., and to Mr G. M. Spooner, for all the help they have so kindly given me.

The majority of the mysids collected during the night were immature and practically all the adults were actively breeding, the males large and well developed and the females with full brood-pouches. The proportion of adults increased markedly in the later hauls. Whilst sorting the collection I was particularly struck by the preponderance of males among the adults. The numbers of the sexes were counted in *Gastrosaccus normani*. I found that in the early part of the night there was an average of three adult males to every adult female, with the sexes more or less evenly balanced in the juveniles. In the later hauls more females appeared and the males outnumbered them by only two to one, while the juveniles were again present in almost equal numbers.

Amongst the specimens of *G. normani* I was interested to find three adults which possessed reflexed lobes on the posterior margin of the carapace but

TABLE I. NUMBERS OF MYSIDACEA SPECIES CAPTURED
IN EACH HAUL OF THE EDDYSTONE CRUISE

Haul ... Time ...	1 8.17- 8.56	2 9.14- 9.45	3 10.01- 10.34	4 10.58- 11.34	5 00.55- 01.31	6 01.51- 02.22	7 02.50- 05.26	8 04.01- 04.36
<i>Anchialina agilis</i>	1	63	181	790	580	480	1290	1430
<i>Schistomysis ornata</i>	—	59	36	120	130	320	260	370
<i>Leptomysis gracilis</i>	3	146	136	510	270	280	740	1160
<i>Gastrosaccus normani</i>	1	{ 24 ♂ 9 ♀ 20 juv.	{ 52 ♂ 17 ♀ 83 juv.	{ 18 ♂ 7 ♀ 23 juv.	{ 11 ♂ 4 ♀ 11 juv.	{ 12 ♂ 7 ♀ 19 juv.	{ 20 ♂ 11 ♀ 15 juv.	{ 13 ♂ 7 ♀ 9 juv.
<i>Erythropus elegans</i>	—	1	—	—	—	2	6 (1 with parasite)	8 (2 with parasite)
<i>Siriella norvegica</i>	—	2	1	—	1 (♀ 23 m.)	1	—	1 (juv.)
<i>S. jaltensis</i>	—	1	—	—	1 (juv.)	—	—	—
<i>Mysidopsis gibbosa</i>	—	2	1	—	1	—	—	—
<i>M. angusta</i>	—	6	—	—	—	—	1	—

which, in every other particular, conformed with the published descriptions of the species. My husband (Tattersall, 1912, p. 41) recorded similar specimens from the west coast of Ireland, and among his unpublished notes I find a record that he had examined a male and a female specimen from Plymouth, both with reflexed lobes, but which were 'undoubtedly *G. normani*'. It was at one time thought that the presence of reflexed lobes was constant for certain species, and that they never occurred in *G. normani*. Acting on this assumption, Kossman (1880, p. 95) founded the genus *Haplostylus* for those species which had no lobes on the posterior margin of the carapace, and he placed *G. normani* in this genus. Since it is now clear that the character upon which the genus was founded is variable the name *Haplostylus* (ἁπλός = simple) ceases to have any significance and the species must be referred to Sars's original genus *Gastrosaccus*.

In the material from haul 7, I found an adult female of *Erythrops elegans*, bearing a large male specimen of the parasitic copepod *Aspidoecia normani* Giard & Bonnier attached by a short stalk to the middle of the dorsal surface of the first abdominal somite. In haul 8, I found two more specimens of *Erythrops elegans* which were parasitized by the same species. One of the *Aspidoecia* was a male attached to the dorsal surface of the second abdominal somite, and the other was a large female with eight to nine ovisacs attached to the first abdominal somite. Among about twenty specimens of *Erythrops elegans* dredged off Rame Head on 6 June 1948, I found one adult female bearing a female *Aspidoecia normani* on the dorsal surface of the second abdominal somite. Only one of the hosts was a male which appeared to be fully developed. It is significant that although unparasitized females captured at the same time all had their brood-pouches full of eggs or embryos, all the parasitized females had empty brood-pouches.

A. normani has been recorded from Norwegian waters on five species of *Erythrops*. Scott (1902, p. 480) recorded it from the Firth of Forth on *E. elegans* and *E. microps* (= *E. goësi*) but, although its host species are known from many localities around our coasts, I can find no further record of it from British waters. Its occurrence in two gatherings taken nearly 12 years apart suggests that it may occur regularly in the Plymouth area.

Although the Eddystone cruise yielded representatives of only nine species, there have, up to the present, been no fewer than twenty-six species of mysids recorded from the Plymouth area. I have therefore drawn up a key for the identification of the genera to which they belong, with supplementary keys¹ from which it should be possible to identify any of the species mentioned. I have included among these a few species which have not yet been recorded from the Plymouth area, but which may reasonably be expected to be found there.

Descriptions of genera and species may be found in the standard works of Sars (1870-9) and Zimmer (1909). The keys given by Zimmer (1933) for the North and Baltic Seas, and in particular the sketches which accompany them, are also very useful.

The nomenclature here conforms with that adopted in the Ray Society Monograph (Tattersall, in Press).

KEY TO THE MYSIDACEA FOUND IN THE PLYMOUTH AREA

Genera

- | | |
|--|---|
| 1. Telson cleft. | 2 |
| Telson entire (one species with very small naked incision). | 8 |
| 2. Scale setose all round. Carpus and propodus of third thoracic limb fused, much enlarged and not subdivided. <i>Heteromysis</i> S. I. Smith [see p. 785] | |
| Scale with outer margin without setae. Third carpopropodite subdivided into three or more segments, not much enlarged. | 3 |
| 3. Exopod of uropod with spines arming outer margin. | 4 |
| Exopod of uropod setose all round. | 5 |

¹ The supplementary keys are given in taxonomic order.

4. Short robust form. Posterior margin of carapace transverse and straight. Inner margin of endopod or uropod with many spines in series right to distal end. Telson with many spines in series. Carpopropodus of thoracic endopods subdivided into three or four segments. *Anchialina* Norman & Scott [*A. agilis* (G. O. Sars)]
Long slender form. Posterior margin of carapace emarginate. Few large spines on inner margin of endopod of uropod. Few spines on lateral margins of telson, not in series. Carpopropodus of thoracic endopods subdivided into many segments. *Gastrosaccus* Norman [see p. 788]
5. Scale ovate, with proximal part of outer margin naked and not ending in a thorn. *Hemimysis* G. O. Sars [*H. lamornae* (Couch)]
Naked portion of outer margin of scale ending in a thorn or spine. 6
6. Scale long, slender, with naked outer margin terminating in articulated spine; its apex little, if at all, longer than spine. Fourth pleopod of male with exopod very long, styliiform, seven-segmented; distal segment terminating in a knob, armed a short distance from its apex with dense, spirally arranged spinules, but no 'pincer' setae. *Praunus* Leach [see p. 787]
Scale oval, its apex extending far beyond terminal thorn. Fourth pleopod of male very long; armed distally with two long setae which form a weak kind of 'pincers'. 7
7. First subsegment of carpopropodus of thoracic limbs short, swollen, very setose and cut off obliquely from more distal joints. *Paramysis* Czerniavsky [see p. 787]
First subsegment of carpopropodus of third to eighth thoracic limbs longer than more distal segments, not swollen and cut off by transverse articulation. *Schistomysis* Norman [see p. 787]
8. Scale with outer margin naked and ending in a thorn. 9
Scale setose all round. 10
9. Telson short, triangular, lateral margins naked, apex narrow, transverse, armed with 2-4 strong spines. Eye pigment very red. *Erythroops* G. O. Sars [see p. 786]
Telson long, linguiform with rounded apex; armed all round with many spines usually arranged in series. Exopod of uropod two-segmented; inner margin of endopod with many spines. *Siriella* Dana [see p. 785]
10. Tarsus, three- to four-segmented. Pleopods of male biramous, natatory, with only setae modified. (Telson long.) 11
Tarsus six- to eight-segmented. Pleopods of male rudimentary; fourth pair long, with modified setae. 12
11. Scale very slender and rather long. Telson more parallel-sided, armed with many spines in series. (Carpopropodus of third to eighth thoracic limbs three-segmented.) *Leptomysis* G. O. Sars [see p. 786]
Scale lanceolate. Telson triangular, tapering to narrow truncate or rounded apex (one British species has small unarmed median notch); lateral margins armed with small spines not in series. (Telson hollowed into a trowel-shape.) *Mysidopsis* G. O. Sars [see p. 786]
12. Scale long and narrow. Telson long, tapering, with many spines arming lateral margins and apex. Fourth pleopods of male very long, armed distally with two equal setae. 13

Scale small and narrow. Telson short, lateral margins unarmed, each ending distally in large spine; apex rounded, armed with dense comb of regular spines. Fourth male pleopod long, with 'pincer' setae. (Eye-stalks long, cylindrical.)

Mesopodopsis Czerniavsky
[*M. slabberi* (van Beneden)]

13. Distal end of scale acutely pointed.

Acanthomysis Czerniavsky
[*A. longicornis* (Milne Edwards)]

Distal end of scale rounded.

Neomysis Czerniavsky
[*N. integer* (Leach). (= *vulgaris* J. V. Thompson)]

Siriella Dana, 1850

1. Rostrum long and tapering, extending to distal end of second segment of antennular peduncle. Apex of telson with four (rarely three) spinules between the two large apical spines. *S. armata* (Milne-Edwards)

Rostrum short and pointed, reaching only half-way along the first segment of antennular peduncle. Telson with three apical spinules. 2

2. Terminal spinules of telson of equal length. Distal segment of exopod of uropod not twice as long as broad. *S. clausii* G. O. Sars

Terminal spinules of telson in form of trident with median one considerably longer than the other two. Distal segment of exopod of uropod twice (or nearly) as long as broad. 3

3. Outer margin of exopod of uropod with 9-15 spines. Spines arming inner margin of endopod of uropod increasing evenly in size distally without smaller spines between. *S. jaltensis* Czerniavsky

Outer margin of exopod of uropod with 11-12 spines. Spines arming inner margin of endopod of uropod arranged in series proximally with the 8-10 distal spines equal and no small ones between. (Rostrum curved downward and appearing short in dorsal view.) *S. jaltensis* var. *brookii* Norman

Outer margin of exopod of uropod with 15-23 spines; spines on inner margin of endopod arranged in series throughout. Very like *S. clausii* in general appearance but nearly twice as large. *S. norvegica* G. O. Sars

Gastrosaccus Norman, 1868

Posterior margin of carapace with fringe of eight to ten delicate prolongations. Antennular peduncle without conspicuous setae. Apex of scale equal in length to terminal spine of outer margin. Telson with 6-8 large spines on each lateral margin. Fifth abdominal segment laterally compressed with median dorsal keel produced into a spine posteriorly. *G. spinifer* (Goës)

Posterior margin of carapace usually with two reflexed lobes. Inner margins of second and third segments of antennular peduncle, each with three to five long plumose setae. Apex of scale shorter than spine terminating outer margin. Telson with 6 spines on each lateral margin. (Endopod of uropod with 6 spines on inner margin.) *G. sanctus* (van Beneden)

Posterior margin of carapace usually without reflexed lobes. Inner margins of second and third segments of antennular peduncle each with a single plumose seta. Apex of scale longer than terminal spine of outer margin. Telson with about 10 spines on each lateral margin. (Endopod of second pleopod of male sigmoid and not natatory. Eyes small.)

G. normani G. O. Sars

Erythrops G. O. Sars, 1869

1. Outer margin of antennal scale serrated. Inner margin of endopod of uropod minutely serrulated under the setae. 2
 Outer margin of antennal scale not serrated. Inner margin of endopod of uropod usually not serrulated. 3
2. Distal serration of outer margin of scale longer than apex of scale. Endopod of eighth thoracic limb variable in length, but not extending beyond posterior margin of abdomen. *E. serrata* (G. O. Sars)
 Distal serration of outer margin of scale shorter than apex of scale. Endopod of eighth thoracic limb reaching beyond distal tip of uropod. *E. abyssorum* G. O. Sars
3. Inner margin of endopod of uropod minutely serrulated. 4
 Inner margin of endopod of uropod without serrulation. (Endopod of eighth thoracic limb extending to posterior end of fifth abdominal segment. Eyes large, close together; short, linguiform rostrum produced forward between the eyes; antennal scale considerably longer than antennular peduncle.) *E. erythrophthalma* (Goës)
4. Eyes large, set well apart, antennal scale a little longer than antennular peduncle. Endopod of eighth thoracic limb usually short, barely reaching end of fourth abdominal segment. (Animals small and comparatively robust.) *E. elegans* (G. O. Sars)
 Eyes small, set widely apart; antennal scale short, subequal in length to the antennular peduncle. Endopod of eighth thoracic limb reaching to posterior end of telson. *E. microps* (G. O. Sars)

Leptomysis G. O. Sars, 1869

1. Integument covered with scales which are upturned distally, giving the animals a hispid appearance. Rostrum acutely pointed with convex sides and a deep notch at each side at its base. (Animals very transparent and slender. Marked constriction in telson marking insertion of distal pair of long marginal spines. Statocyst large.) *L. gracilis* (G. O. Sars)
 Integument smooth. Rostrum without lateral notches. 2
2. Animals longer and more slender. Body covered all over with fine branches of brown pigment. Rostrum with straight sides. (Limbs stouter and statocyst smaller than in *L. gracilis*. No marked constriction in the telson.) *L. mediterranea* G. O. Sars
 Animals much shorter, more compact and robust than other two species. Colour milky, pale rosy markings. Rostrum short, with curved margins. (Eyes closely set, thick and short. Telson short and broad without constriction distally.) *L. lingvura* (G. O. Sars)

Mysidopsis G. O. Sars, 1864

1. Telson with no trace of median cleft. 2
 Apex of telson with short unarmed notch. (Lateral margins of telson armed with 14-18 spines which increase in size distally. Cleft wedge-shaped without plumose setae.) *M. angusta* G. O. Sars
2. Rostrum broadly triangular. Telson triangular, rather long; lateral margins straight, converging to narrow truncate apex with a large spine at each

corner; 8-10 spines on each lateral margin. Carapace without median swellings.

M. didelphys (Norman)

Rostrum very small, in form of very obtuse triangle. Telson short, with lateral margins concave, narrowing to rounded apex armed with two small median spinules; spines on lateral margins very small. Two conspicuous median swellings on carapace appearing as humps in lateral view.

M. gibbosa G. O. Sars

Paramysis Czerniavsky, 1882

Short robust form; length 7 mm. Uropod armed along whole length of inner margin with 28-30 spines arranged in series. Telson narrow, with narrow cleft not widely open.

P. arenosa (G. O. Sars)

Longer and more slender form; length 11 mm. Endopod of uropod with 9-10 subequal spines along distal two-thirds of inner margin. Telson wider, cleft widely open with sides nearly straight.

P. helleri (G. O. Sars)

Schistomysis Norman, 1892

Note. The spines arming the inner margins of the endopods of the uropods are fewer and less crowded, and the cleft of the telson less deep in immature animals than in adults in this genus. As a result there may be some difficulty in identifying immature specimens.

1. Eyes long and narrow. Carpopropodus with nine subsegments. (Body very slender, especially anteriorly. Cleft of telson fairly wide with straight sides. Spines arming inner margin of endopod of uropod very dense.)

S. spiritus (Norman)

Eyes not long and narrow. Carpopropodus with five to six subsegments. . . 2

2. Eyes short and thick and large, not extending much beyond lateral margin of carapace. Spines arming inner margin of endopod of uropod not dense; one situated terminally, then a space, then 1 spine, then another space and then regular row to statocyst. Carpopropodus with five subsegments (rarely six). (Body robust. Cleft of telson deep with convex margins.)

S. ornata (G. O. Sars)

Eyes nearly globular, moderately large. Endopod of uropod markedly curved, armed on inner margin with 1 very long terminal spine, then a gap to about half-way along margin, then 3-4 very long slender spines, and then a close row of spines in series back to the statocyst. Carpopropodus with six subsegments (rarely five).

S. parkeri Norman

A fourth species, *S. kervillei* (G. O. Sars), has not yet been recorded from Plymouth, though it has been taken in the mouth of the Seine and off the coast of Kent. It is very closely similar to *S. ornata* and appears to have similar habits to that species. Although certain of its characters are quite constant, and the two species may be distinguished when they are together, it is extremely difficult to set out shortly any definite characters whereby they may be distinguished. The most reliable guide is in the arrangement of the chromatophores.

Praunus Leach, 1814

Note. The specific characters differentiating the species of this genus are not attained until the animals are fully grown, though they may be sexually mature. The proportions of the antennal scale, the number of sub-segments in the tarsus of the thoracic limbs and the depth

of the cleft of the telson vary considerably with age, and it is very difficult to distinguish between specimens of *P. flexuosus*, which are not fully mature, and specimens of *P. neglecta*. The only reliable guide lies in the distribution of the chromatophores, which remains constant throughout life (Keeble & Gamble, 1904, p. 331).

1. Apex of scale shorter than terminal spine of outer margin. (Body long and slender. Eyes well developed with long cylindrical eye-stalks; whole of cornea and part of eye-stalks extending well beyond lateral margins of carapace. Scale very long and slender, seven to nine times as long as broad; more than twice as long as antennular peduncle. Telson cleft to one-sixth of total length. Endopod of uropod with 10-12 spines on inner margin. Tarsus of third to eighth thoracic limbs usually with six subsegments, eighth with five.) *P. flexuosus* (Müller)
2. Apex of scale longer than terminal spine of outer margin. Somewhat smaller than *P. flexuosus*, but very similar in form. Antennal scale five times as long as broad; less than twice as long as antennular peduncle. Apex slightly longer than terminal spine. Endopod of uropod with 12 spines on inner margin. Telson cleft to one-fifth of total length. Tarsus of thoracic limbs five-segmented (eighth four-segmented). *P. neglectus* (G. O. Sars)

Body shorter and less slender than preceding species. Antennal scale four times as long as broad, and about one-third longer than the antennular peduncle. Apex produced beyond terminal spine to about two to three times length of spine. Endopod of uropod with 6-7 spines on inner margin. Telson cleft to nearly one-third of total length. Tarsus of thoracic limbs four-segmented. *P. inermis* (Rathke)

Heteromysis S. I. Smith, 1874

1. Telson with spines only on the distal portion of the lateral margins. 2
Telson with spines (18-20) along whole length of lateral margins; apical lobes with 2 spines, the inner longer than the outer. Endopods of uropods with spines along whole length of inner margin. *H. armoricana* Nouvel
 2. Endopod of uropod with 17-20 spines along whole of inner margin. Lateral margins of telson with 14-18 spines on distal portion; apical lobes with 2 spines, the inner longer than the outer. Eye not very small. *H. formosa* S. I. Smith
- Endopod of uropod with single spine near statocyst. Lateral margins of telson armed distally with 9-13 spines; apical lobes narrow and acute, armed with 2 spines, the outer twice as long as the inner. Eyes very small. *H. microps* (G. O. Sars)

SUMMARY

The mysid fauna of eight night hauls made near the Eddystone Lighthouse is analysed.

Keys are given for the identification of Mysidacea which have been recorded from, or are likely to occur in, the Plymouth area.

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THE FOOD OF THE DOGFISH, *SCYLIORHINUS CANICULUS* L.

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During the past eight years records have been kept of the contents of the stomachs of all dogfish dissected in the Zoology Department of Reading University. The specimens, numbering about 450 altogether, came from Swansea Docks, and were caught off the west coasts of the British Isles. Students were asked to spread out the contents of the stomach of the fish they were dissecting in a dish, and to make notes of those animals they could identify. I then, as far as was possible, checked the identifications, and removed for more detailed investigation any specimens of particular interest. In the circumstances it was impossible to make accurate numerical records of each species, or to work out fragments from partially digested material, but the rare specimens were recorded by numbers. Sometimes a record of one means one perfect specimen.

The records showed a remarkable uniformity, indicating either a habit on the part of the fish of hunting over certain bottom areas, or a selective search for palatable food. Six phyla were represented, and despite partial digestion, the genus and sometimes the species could be determined. Details are given in Table I.

Comparing these records with those of Ford (1921), there is a close resemblance in the nature of the food, allowing for variations due to the location of the feeding grounds. Several points of interest may be noted:

(i) Fish comprise only a part of the food of the dogfish and consist of small specimens. As Ford points out, dogfish are bottom feeders, and the presence of pelagic fish in the stomach is largely accidental.

(ii) Ford's records do not include the horse mackerel, which in my records for 1948 and 1949 were almost as numerous as herring. The scutes on this fish retard digestion and it is therefore easy to identify.

(iii) In the Invertebrate groups we have many records in common—some of relatively rare animals, e.g. *Atelecyclus* and *Gonoplax*, and others indicating a selective feeding habit, e.g. *Upogebia*, *Thyone*, Gephyrean worms.

(iv) Molluscs, except for *Buccinum*, are not well represented. How does the dogfish tackle a whelk? Does it swallow it whole, and dissolve the shell? I have found lamellibranch shells and even cuttlebone undigested, but have never seen a trace of a whelk shell, though opercula are frequently found. Are the opercula scooped up from dead material on the sea bottom? Similarly,

does the dogfish swallow the shell containing the hermit crab—for again, no trace of the shell remains, though the crab itself forms a large proportion of the food in some fish?

TABLE I. SPECIES RECORDED FROM STOMACHS OF
Scyliorhinus caniculus

	1942	1943	1944	1945	1946	1947	1948	1949
Phylum Chordata: class Pisces								
<i>Clupea harengus</i> (6 or more records)	×	×	×	×	×	×	.	×
<i>Trigla lucerna</i>	.	.	.	I	.	.	.	.
<i>Limanda limanda</i>	.	.	.	.	.	.	I	.
<i>Cottus bubalis</i>	.	.	.	.	.	.	.	I
<i>Caranx trachurus</i>	.	.	.	.	.	.	3	4
<i>Nerophis lumbriciformis</i>	.	.	.	.	.	.	.	I
Egg capsule of dogfish	.	I	.	.	.	.	.	.
Phylum Annelida: Chaetopoda, Polychaeta								
<i>Aphrodite aculeata</i>	.	.	.	5	.	.	.	.
<i>Nereis</i> sp.	.	.	.	2	.	.	.	.
<i>Nephtys</i> sp.	.	I	.	.	.	.	.	.
<i>Glycera lapidum</i> ?	I	.	.	.	.	.	10	4
<i>Lumbriconereis latreilli</i>	.	.	I	.	.	.	5	.
Phylum Gephyrea								
<i>Phascolosoma</i> sp.	.	.	.	.	.	.	I	I
Phylum Echinodermata: class Holothurioidea								
<i>Thyone fusus</i>	2	.	3	8	.	.	.	3
Phylum Arthropoda: class Crustacea								
<i>Hippolyte varians</i>	.	.	.	I	.	.	.	.
<i>Leander serratus</i>	.	.	.	.	.	.	.	2
<i>Crangon vulgaris</i>	I	I	I	.	.	.	I	.
<i>Homarus vulgaris</i> (small)	.	6	.	.	.	.	.	.
<i>Nephrops norvegicus</i>	.	.	.	.	.	.	I	20
<i>Galathea</i> spp.	.	.	.	.	.	.	.	I
<i>Upogebia stellata</i>	.	.	3	.	.	.	.	.
<i>Eupagurus bernhardus</i> (many)	×	×	×	×	×	×	.	×
<i>Portunus</i> , mainly <i>depurator</i>	.	3	.	.	.	.	.	.
<i>Atelecyclus septemdentatus</i>	.	.	.	.	.	.	2	.
<i>Gonoplax rhomboides</i>	.	I	.	.	.	.	.	3
Phylum Arthropoda: class Pycnogonida								
<i>Pycnogonum littorale</i>	.	I	7	.	.	.	.	.
Phylum Mollusca: class Lamellibranchia								
<i>Mya truncata</i> (siphons)	.	.	.	2	.	.	.	.
<i>Ensis ensis</i> (shell and siphons)	.	.	.	I	.	.	.	.
Phylum Mollusca: class Gastropoda								
<i>Buccinum undatum</i> (opercula)	Many	.	.	Many	.	.	.	.
Phylum Mollusca: class Cephalopoda								
<i>Sepia officinalis</i> —small	.	.	2	.	.	.	I	.
beaks of adults	.	.	.	Many	.	.	Many	.
<i>Loligo forbesii</i>	.	.	.	.	.	.	I	.
<i>Octopus</i> (acetabula)	Many	.	.	.	.	.	.	.

(v) There is no mention of *Nephrops norvegicus* in Ford's records. This is not surprising, for his fish came from the English Channel where there are none of the extensive muddy bottoms which these lobsters require. In fact, *Nephrops* is not recorded in the Plymouth Fauna list. In my records, it appeared for the first time in 1948, and in 1949 was abundant. I wrote to the fish merchant from whom the fish were obtained, asking for information

concerning the fishing grounds. He replied that only during the past two years had the usual grounds, closed on account of mine fields during the war, been re-opened. Recently fish had been caught in the Irish Sea and off the extreme west coast of Ireland, to a distance of 400 miles west of Swansea. Muddy areas are present to the north and west of the British coasts, and the dogfish were evidently feeding on these grounds.

Collating the above information, it appears that the favourite food of the dogfish consists of a mixture of whelks, shrimps, hermit crabs, cuttlefish, *Thyone*, and small fish of various species. They are general feeders on benthic and pelagic animals, scooping some up from the bottom and catching others while swimming. There is no evidence that they are a serious danger to the food fishes.

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THE OCCURRENCE OF BRITISH *APLYSIA*

By Ursula M. Grigg¹

From the Plymouth Laboratory

(Plates I and II and Text-figs. 1-3)

INTRODUCTION

On 13 November 1947 a specimen of the sea hare, *Aplysia depilans* L., which had been trawled in Babbacombe Bay, was sent to the Plymouth Laboratory. When it was realized that the animal was not the common *A. punctata* Cuv., collecting trips to likely places were undertaken in the hope of finding more. No others were found, but on one of the expeditions Dr D. P. Wilson picked up a specimen of *A. limacina* L.

Both *A. depilans* and *A. limacina* are found in the Mediterranean and on the west coast of Europe: *A. depilans* has been found in British seas before, but so far as is known *A. limacina* has not.

These occurrences provide the main reason for publishing this study. The paper also includes an account of the distribution of aplysiids in British waters and a review of the controversy over the identity of large specimens. As the animals are not usually described in natural history books, notes on the field characters are added.

I would like to thank the Director of the Plymouth Laboratory for affording me laboratory and collecting facilities and for his interest in the work. I am most grateful to Dr G. Bacci, who went to much trouble to send me specimens from Naples; to Dr W. J. Rees, who arranged for me to have access to the British Museum collection; to Dr D. P. Wilson, who has provided the photographs of *A. punctata* (Pl. I) and *A. limacina* (Pl. II); and to D. J. Slinn, who prepared the map. The distribution records were compiled with the help of many members of other marine laboratories and university zoology departments, and I am indebted to them for their kind co-operation in answering my queries.

I am greatly indebted to the Director of the Stazione Zoologica, Naples, for allowing me to spend a fortnight at the Stazione in September 1949, and providing me with living specimens of *A. limacina*.

This study was undertaken during the period of tenure of a D.S.I.R. grant.

RECENT OBSERVATIONS

Aplysia depilans

The specimen of *A. depilans* was trawled by a Teignmouth fishing vessel in Babbacombe Bay on 12 November 1947. It was brought to the Plymouth Laboratory on 13 November in a rather damaged condition.

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When crawling the animal measured 24 cm. and was therefore a large specimen. It was a purplish fawn colour, with darker and lighter mottlings. The lips, gills and genital aperture were pale fawn. The eyes were very small and black, each surrounded by an area of pale blue. No dye was ejected, even when the animal was handled. It was put in a tank with circulating seawater, and crawled a short distance very slowly, without attempting to feed. The footsole was broad and non-contractile, and the head was not lifted or stretched out. The parapodia, which were low and exposed the visceral hump, were not undulated. The slight side to side swaying of the head and neck as the animal advanced was more reminiscent of a hippopotamus than a hare.

After the death of the specimen two days later, dissections showed that the head and visceral mass were much bruised. The shell was torn at the apex, which did not appear to have been pronounced. The anal indentation was also shallow. The shell was 5.7 cm. long and 4.5 cm. broad, measurements being taken from the apex to the farthest margin, and from the shoulder to the opposite margin at right angles to the first measurement. Only the hyaline layer of the shell was present. The radula was of the spade-shape characteristic of the species and carried over 70 rows of teeth; the formula was not determined. There was no recognizable food in the oesophagous or gizzard.

The photograph (Pl. I), which was taken when the animal was dying, is included to show the shape of the head and parapodia. The bloating of the footsole is not characteristic of a healthy specimen.

Aplysia limacina

The specimen of *A. limacina* was collected at L.W.S.T. on the Salstone, Salcombe Estuary, on 15 February 1949. It measured 20 cm. extended, which is small for the species.

The animal was a dark purple, the skin having a velvet lustre. The edges of the parapodia, tentacles and mouth-lappets were violet, as was the dye, which was ejected copiously whenever the animal was disturbed. The eyes were black.

This *Aplysia*, though sluggish, could be made to crawl by handling or by warming the water slightly. When it was at rest, the parapodia were folded over one another, and exhibited slow waving movements. A water current flowed from front to back through the cavity thus formed above the mantle. When crawling, the animal held the parapodia partially or fully stretched up, undulating the edges. The mouth-lappets and rhinophores were also in constant motion, but the head was never lifted and held out as in *A. punctata*. The footsole was narrow and the animal sometimes gripped the substratum with the posterior end only, as *A. punctata* does, but was not capable of the active extension and contraction of that species.

Specimens in the Naples Aquarium also folded their parapodia across their mantles when at rest and passed water over the visceral mass by undulating

the parapodia. When an animal was crawling the parapodia were partially extended, while in swimming they waved vigorously, propelling the *Aplysia* forward. The long axis of the body was held nearly vertical when the animal swam across the tank with the head slightly advanced and the tail bent back, giving a graceful sigmoid curve to the foot. When the animal swam a short distance over the tank floor the foot was horizontal.

Though the Salcombe specimen browsed on *Ulva lactuca* when first caught, it lost weight rapidly and was killed 3 weeks later. The shell had both hyaline and calcareous layers, and the apex and anal indentation were pronounced. It measured 3.5 cm. long by 2.8 cm. broad. The radula was of the typical square shape with abrupt tip, but was rather short, measuring only 0.8 cm. long by 0.9 cm. broad (Text-fig. 2C). There were 28 rows of teeth, and the formula across the broadest part was 20.1.20. The long dagger-like cusps on the lateral teeth were very well developed, which suggests that it was a young specimen. There was no recognizable food in the gut.

Dr Wilson's photograph (Pl. II) was taken while the animal was crawling with parapodia partially extended.

HISTORY

Although *Aplysia punctata* is the only aplysiid common in British seas, it has been described under several names on account of the great variation between individuals. Owing to their lack of skeletal structure compared with most shell-bearing molluscs, all aplysiids can assume many shapes, a faculty increased in *A. punctata* by its power of extension, which exceeds that of most other members of the family. The colour varies from a dark purple to a pale olive green, always with well-defined spots of black or white, and occasionally with the parapodia bordered with blue. Young specimens may be a delicate leaf-green or rose pink, the latter phase being *A. rosea* of Rathke and *A. nexa* Thompson. These colour variations probably depend upon the colour of the weed on which the individuals are living.

In the radula the number of tooth rows and the number of lateral teeth in each row increase as the animal grows larger. Hunt (1878) gives a table of radula formulae in which the numbers range from 4.1.4 to 15.1.15. Though the shape of the radula does not change, the teeth in large specimens are blunt, and rarely have the regular and distinctive shapes of most published diagrams. The shells of large animals show the same phenomenon, being generally coarser and less easy to define than those of small ones. Comparable changes are found in all members of the family.

All these factors have contributed to confuse the synonymy of *A. punctata*, and it is not surprising that on the rare occasions when extra large specimens appeared some naturalists were unwilling to assign them to another species. It was not until descriptions were published from regions where several species were common that the identifications could be made with certainty.

Pennant (1812) gives two species of *Aplysia* in his British list. These he calls *A. depilans* L. and *A. mustelina* Davies. He separates them on the gill shape, and mentions that *A. mustelina* had a crimson patch on 'that part which by its situation corresponds with what Bohadsch deems the lungs in his subject'. Mazzarelli (1893) considers Pennant's *A. depilans* to be *A. punctata*, and his *A. mustelina* to be *A. depilans* Cuv., presumably on the strength of the crimson patch. *A. mustelina* is usually taken to be a synonym for *A. punctata*.

Forbes & Hanley (1853), in their *British Mollusca*, include only one species, which they call *A. hybrida* Sowerby (= *A. punctata*). Jeffreys (1869), while supporting their view that *A. punctata* is the common species, records two specimens of *A. depilans*, one from Guernsey, and one collected by Gosse in Torbay.

In 1870 Couch described two specimens under the name of *A. melanopus*. His types are in the British Museum and are undoubtedly *A. depilans*.

In the autumn of 1875 A. R. Hunt, who had made a collection of shells and radulae of *A. punctata* from Torbay, found several *A. depilans*. He published an account of these (Hunt, 1877), and discussed their identity. While considering the possibility that they might be *A. depilans*, he remarked that 'too much reliance is perhaps placed on specific differences deduced from the very flexible shells and varying odontophores of these gastropods', and pointed out that 'an examination of a series of specimens of different sizes will prove conclusively that the odontophores develop gradually with the growth of their owners'. After collecting more in the winter of 1877-78 he published a paper (Hunt, 1878) on the growth of aplysiids, in which he came to the conclusion that the specimens were overgrown *A. punctata*. This paper includes an ingenious theory to account for the fact that all these large specimens were found in the winter when *A. punctata* was not present, and that there were no specimens within the size range of *A. punctata* which could be considered as the young of another species. He therefore suggested that *A. punctata* could only reach maximum size when protected from rough seas and provided with abundant food. These conditions were fully met near Torquay, which was sheltered naturally from the north and west and where artificial breakwaters of various kinds provided additional protection. Ample food was to be found on the *Ulva* beds growing round the sewage outflow at Tor Abbey. The animals were therefore able to live longer than they would otherwise have done, and to attain a large size. Hunt went on to remark that 'as the large *Aplysiae* have not been taken in deep water . . . it is probable that they do not make their way back to the greater depths from which they originally came and that the race is kept up by partially grown individuals'. Apparently he did not realise that *Aplysia punctata* comes inshore to spawn. He did not comment on the different external appearance and lack of contractility of his large animals as compared with *A. punctata*, though he mentioned that they very rarely ejected dye.

Garstang (1890), who discussed the subject with Hunt and examined his specimens, was equally inclined to regard them all as *A. punctata*, but he said: 'I trust that the subject may receive more conclusive treatment in the hands of a naturalist upon a coast where large Aplysiae are more common than they are with us in England.'

This treatment was supplied when Mazzarelli published his monograph (Mazzarelli, 1893) describing the anatomy, field characters, distribution and habits of six aplysiids including the three considered here. He recognized three records of *A. depilans* for the British coast. These are Gray (reference not given), Pennant (1812), and Couch (1870). He did not include Britain in his list of localities for *A. limacina*.

In the second edition of the list of British marine mollusca published by the Conchological Society of Great Britain and Ireland in 1902, *A. punctata* and *A. depilans* are both included, but in the later list compiled by Winckworth (1932) only *A. punctata* appears.

DISTRIBUTION

Aplysia punctata

This is a widely distributed species ranging from the Canary Islands to the Arctic Circle. It is found on the coasts of Italy, Sicily, Corsica, Algeria, south and west coasts of France, coasts of Ireland, England, Greenland and possibly Mauritius (Mazzarelli, 1893); Norway (Sars, 1878); Sweden, Portugal (British Museum collection); Heligoland, Holland, Belgium (Hoffmann, 1926); Roscoff (Dautzenberg & Fischer, 1925), the Channel Isles (Jeffreys, 1869; Sinel, 1906), and Japan.

Round most of the British Isles *A. punctata* is common. It is most abundant where the water is clean, but occurs in estuaries where there is little pollution. Many of the records refer to specimens seen on the shore during the breeding season, some are from dredgings and trawlings, and a few are from crab-pots. One, caught in a surface plankton net, was possibly on drifting weed (Sikes, 1905). The species is abundant in some years and rare in others.

This account of the British distribution has been compiled from local literature, the British Museum collection and many private communications, but is undoubtedly incomplete. The clustering of records reflects the activities of marine stations and individual collectors, but in the neighbourhoods of Hunstanton (Norfolk), Burnham-on-Crouch (Essex), Whitstable (Kent) and on the coast of Glamorgan several naturalists state that they have not yet seen the species.

In the United Kingdom, *A. punctata* is reported from the coasts of Dorset, Devon, the Channel Isles, Cornwall, the Scilly Isles, Somerset, Lundy Island, Pembroke, Cardigan, Caernarvon, Anglesey, the Isle of Man, Argyll, Arran,



Text-fig. 1. Records of British *Aplysia*. ●, *A. punctata*; ▲, *A. depilans*; ✕, *A. limacina*.

Islay, Mull, Cumbræ, the Outer Hebrides, Sutherland, the Orkneys, the Shetlands, Moray Firth, Banff, Aberdeen, Fife, the Firth of Forth, East Lothian, Berwick, Northumberland and Yorkshire. For the seas between Scarborough (Yorkshire) and Selsey Bill (Sussex) no records have been found; there is one doubtful record for Hampshire depending on a specimen identified in a boat and subsequently lost. On the French coast of the Channel it certainly occurs at Dinard and Roscoff.

Thompson (1856) says that the species is common all round the coast of Ireland. More explicit records are for Belfast Lough (Thompson, 1856) and the coasts of Dublin (Colgan, 1908), Cork and Galway (Sikes, 1905).

Aplysia depilans

This species is recorded from the coasts of Italy, Sicily, Corsica, England, Madeira, the west coast of France and the Cape of Good Hope (Mazzarelli, 1893). It is also found on the coasts of Spain and Portugal (British Museum collection), at Roscoff (Dautzenberg & Fischer, 1925), in the Channel Isles (Jeffreys, 1869; Sinel, 1906), and in Torbay (Gosse, recorded by Jeffreys, 1869; A. R. Hunt, 1877, 1878).

British specimens examined during the course of the present study are as follows:

British Museum specimens:

1850. 6. 17. 12, from Weymouth. This animal is interesting as it measures 9 cm. preserved, and is therefore small enough to be directly comparable with specimens of *A. punctata*. It shows very clearly the characters which help to distinguish the two species.

1860. 11. 28. 1, a very large specimen from Ichen, Southampton [presumably the river Itchen].

1870. *A. melanopus* Couch, type specimens, from Polperro.

Other specimens:

The animal from Babbacombe recorded above (p. 796).

Aplysia limacina

Mazzarelli lists this species from the coasts of Italy, Sicily, Corsica, Algeria and the south and west coasts of France. There are specimens from the coasts of Spain and Portugal in the British Museum.

The only British animal, as far as is known, is the specimen from the Salcombe Estuary, recorded above (p. 796).

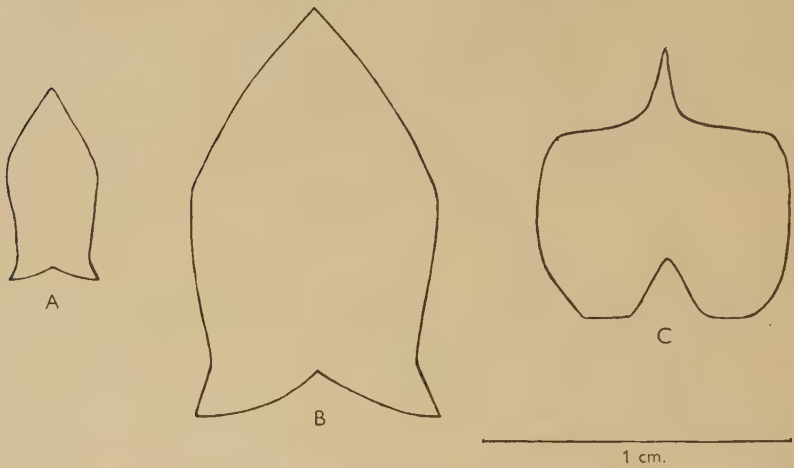
RECOGNITION CHARACTERS

The following characters are included as means of determining the species quickly. Nearly all are external, and have been found to be adequate for the determination of both living and preserved material. The animals from which

the list was made include at least two thousand *A. punctata* brought into the Plymouth Laboratory this year, and preserved material of all three species, including young, from Naples.

Colour, as indicated before, varies considerably and is not reliable. *A. punctata* is the only species which has small well-defined black or white spots, and none of the specimens that have been examined alive lacked them. *A. depilans* and *A. limacina* may be mottled, but the patches do not have such sharp edges. Neapolitan *A. limacina* were sometimes clearly enough marked to be mistaken for *A. punctata* at a first glance. *A. depilans* sometimes has patches of red, blue or yellow round the mouth, penis and gill. All the species go a dirty grey when preserved.

The most easily observed characters refer to the parapodia, mantle and head.

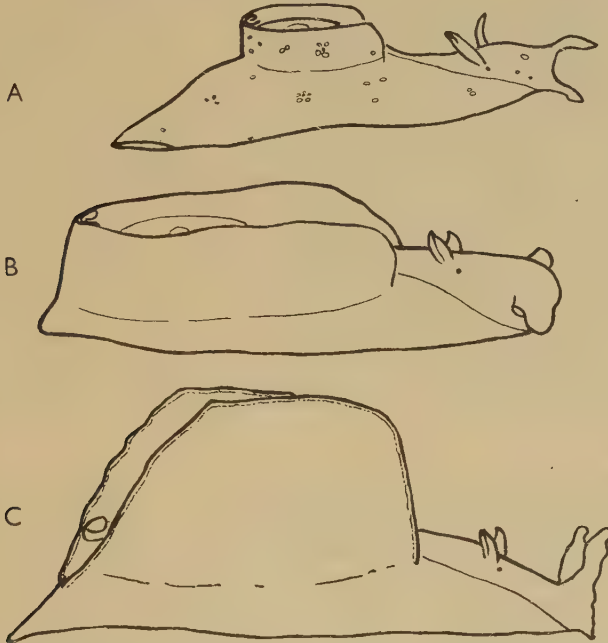


Text-fig. 2. Outlines of radulae of *Aplysia*. A, *A. punctata*; B, *A. depilans*; C, *A. limacina*. From specimens 6, 8.9 and 8 cm. long when preserved, respectively.

A. punctata and *A. depilans* have the parapodia fused at the posterior end. Both have a wide aperture through the mantle above the shell. In *A. punctata* (Text-fig. 3A) the parapodia surround the visceral mass closely and do not extend in front of it to any noticeable degree. As a result the neck is fairly long and there is a long pointed tail posteriorly. In *A. depilans* (Text-fig. 3B) the parapodia stand farther out, along the sides, and extend along the neck for some distance forward of the shell. They are not tall enough to conceal the shell, and the tail is very short and blunt. The parapodia of *A. limacina* (Text-fig. 3C) are separate for the whole of their extent, and there is a gap between the roots of them at the posterior end. They are much larger than in either of the other species, and fold over to conceal the visceral mass completely. The mantle aperture is in the form of a small papilla or siphon which is usually closed in life and has been closed in all preserved specimens examined. In other

respects this species is intermediate between the other two, as the parapodia extend a short way in front of the shell, and there is a short pointed tail.

The mouth-lappets are least developed in *A. depilans*, and both tentacles and rhinophores are short and stout. In *A. punctata* the mouth-lappets are not very large, but the rhinophores and tentacles are slim and are capable of very great extension. The tentacles of *A. punctata* are slit at the tips only, while those of the other two species are slit from the tips nearly to their proximal ends. The mouth-lappets of *A. limacina* form large frills, confluent with similar frills on the rhinophores. The tentacles are short and slender.



Text-fig. 3. General body outlines, showing specific distinctions. A, *A. punctata*; B, *A. depilans*; C, *A. limacina*.

The footsoles of *A. punctata* and *A. limacina* are narrow, while that of *A. depilans* is broad. *A. limacina* can attain 38 cm. in length expanded: *A. depilans* reaches 28–30 cm., and *A. punctata* is generally 15–20 cm. long.

The shape of the radula is characteristic (Text-fig. 2), being long and slim with a gradually tapering tip in *A. punctata*, broader in *A. depilans*, and square with an abrupt tip in *A. limacina*. The numbers of tooth rows and of lateral teeth in each row in the radulae of adult specimens may assist in identification. Mazzarelli (1893) gives these as 38–40 rows with (15–18).I. (15–18) teeth per row for *A. punctata*, 76–80 rows with (30–33).I. (30–33) teeth per row for *A. depilans*, and 82 rows with (40–45).I. (40–45) teeth per row for *A. limacina*.

Fuller descriptions of these animals may be found in Eales (1921), and Mazzarelli (1893). The specific names used in this paper are taken from the latter, which was the original means of identifying the specimens recorded above.

KEY TO SPECIES

Parapodia fused at posterior end: mantle aperture open.

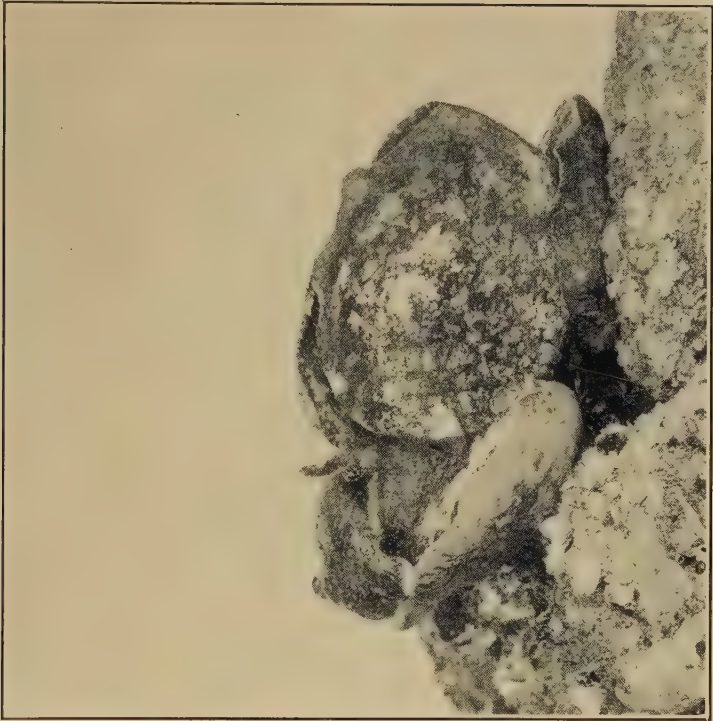
Parapodia do not extend noticeably forward of the shell: tail long. Colour olive green, brown or purple: clusters of well-defined black or white spots. Tentacles long, tubular, each with a slit at the tip. Mouth-lappets distinct, not large. Footsole narrow. Powers of contraction marked. Reaches 20 cm. in length. *A. punctata* Cuv.

Parapodia extend well forward of the shell: tail very short and blunt. Body brown or grey, sometimes with a purple tinge: blotchy but never with well-defined spots. May have coloured patches, round orifices and gill. Tentacles blunt, slit from tip nearly to base. Rhinophores very blunt, mouth-lappets small. Footsole broad. Powers of contraction slight. Reaches 28 cm. in length. *A. depilans* L.

Parapodia separate along their entire length: mantle aperture on a papilla. Parapodia extend forward of the shell: tail short and pointed. Colour usually a dark purple, sometimes mottled: frequently has violet edges to parapodia, tentacles, etc. Tentacles slender, short, slit from tip nearly to base. Rhinophores developed into wide frills: mouth-lappets also long and waving. Footsole narrow. Contractility not so marked as in *A. punctata*. Reaches 38 cm. in length. *A. limacina* L.

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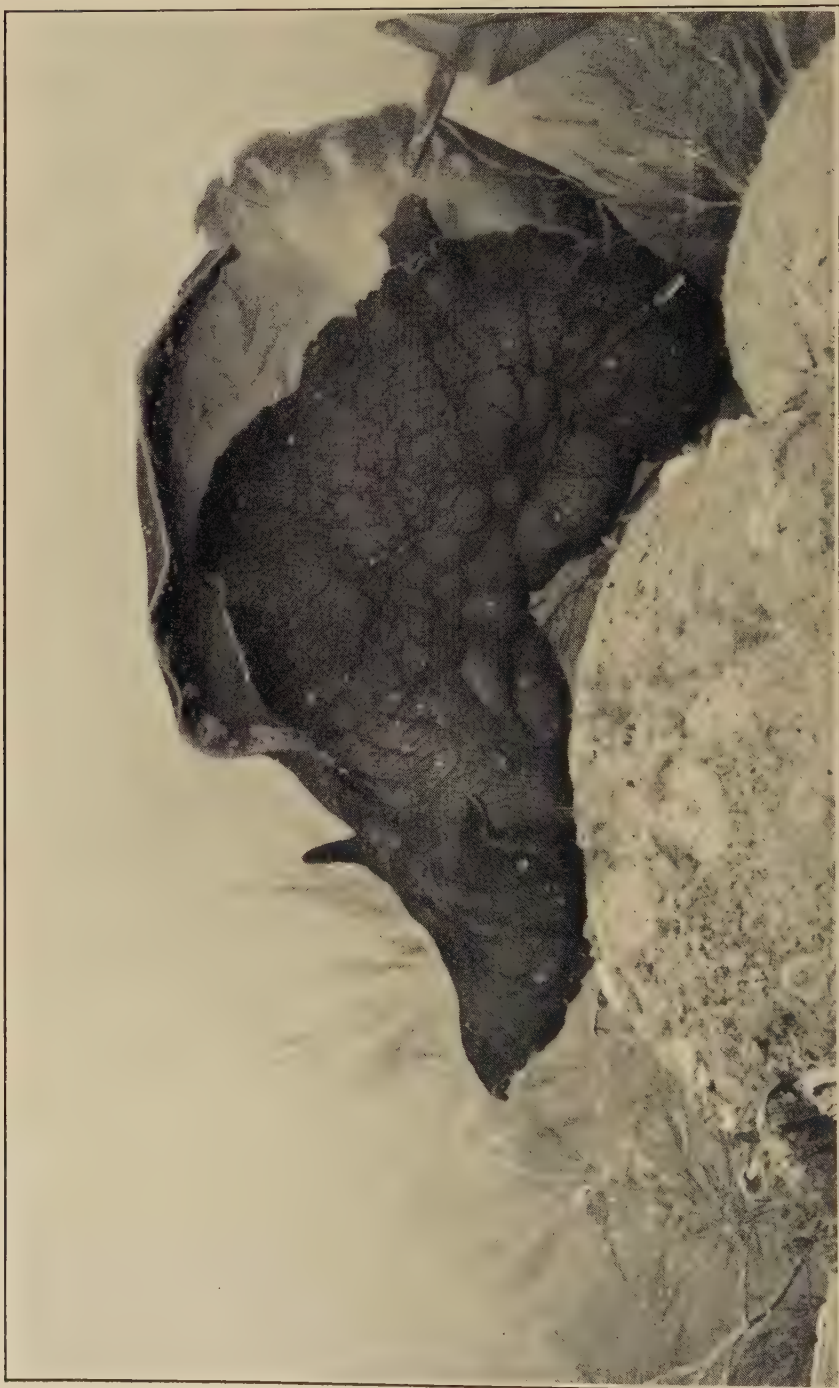
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Aplysia depilans



Aplysia punctata



Aplysia limacina

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EXPLANATION OF PLATES

PLATE I

Photographs of living *Aplysia punctata* ($\times \frac{1}{8}$) and *A. depilans* ($\times \frac{3}{8}$).

PLATE II

Photograph of living *Aplysia limacina* ($\times \frac{1}{2}$).

NOTES ON THE PLYMOUTH MARINE FAUNA

CHIRONOMIDAE (INSECTA:DIPTERA)

By R. E. Hall

The following records were obtained during a fortnight at the beginning of April 1949. The localities investigated were rocky shorepools below the Laboratory, and a small area at the upper tidal limit of Tamerton Lake. In addition to imagoes collected on the wing, larvae were reared from a mud sample taken from the stream bed just below the upper limit of tidal penetration. None of the Tamerton species are marine in the strict sense adopted by Edwards (1926), but those bred out are tolerant of brackish water and belong to the estuarine fauna.

Of the species mentioned none occur in the Plymouth Marine Fauna (Mar. Biol. Assoc., 1931), but *Thalassomyia fraunfeldi* has been recorded from Wembury (Colman, 1940).

Subfamily ORTHOCLADIINAE

Cricotopus fucicola (Edw., 1926)

Plymouth rocky shore pools, both intertidal and above high-water level (emergence from former observed), 15 ♂♂ and 4 ♀♀.

Cricotopus obnixus (Walk.)

Tamerton Lake, ♂ and ♀.

Spaniotoma (Smittia) thalassophila (Goet.)

Plymouth rocky shore pools, intertidal and above high-water level, 8 ♂♂ and 4 ♀♀.

Spaniotoma (Smittia) contigens (Walk.)

Tamerton Lake, 6 ♂♂ taken from swarm at edge of stream at head of creek.

Metriocnemus picipes Mg.

Tamerton Lake, one ♂.

Metriocnemus impensus Walk.

Tamerton Lake, pair *in coitu*.

Tanytarsus (Micropsectra) brunnipes (Zett.)

Tamerton Lake, adults taken in flight, and several bred from larvae living in the mud at the head of the creek.

Subfamily CLUNIONINAE

Thalassomyia fraunfeldi (Schin.)

Plymouth, shore below Laboratory, ♂ on damp seaweed about M.T.L.

Subfamily DIAMESINAE

Prodiamesa olivacea (Mg.)

Tamerton Lake, 2 ♂♂ bred from sample of mud.

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HALACARIDAE (ARACHNIDA:ACARINA)

By H. C. Fountain

The nomenclature follows André (1946). No Acarina were listed in the Plymouth Marine Fauna (Mar. Biol. Assoc., 1931), but *Hydrogamasus littoralis*, *Rhombognathus pascens*, *R. seahami*, and *Halacarus basteri* have since been recorded from Wembury (Colman, 1940).

Species marked with an asterisk are new records for the British Isles.

Rhombognathus (s.s.) *notops* (Gosse)

Plymouth Laboratory tank. Drake's Island.

Rhombognathus (s.s.) *magnirostris* Trouessart. Drake's Island.*Rhombognathus* (*Rhombognathides*) *pascens* (Lohmann)

Wembury, Port Wrinkle. Seaton beach.

**Rhombognathus* (*Rhombognathides*) *trionyx* Trouessart

One, Looe Harbour at low-water level.

Rhombognathus (*Rhombognathopsis*) *seahami* (Hodge)

Plymouth Laboratory tank. Port Wrinkle. Seaton beach.

Subfamily HALACARINAE

Halacarus (s.s.) *ctenopus* Gosse. Duke Rock, Plymouth.*Halacarus* (*Halacarellus*) *basteri* (Johnston). Port Wrinkle.

Copidognathus (s.s.) *fabriciusi* (Lohmann). Port Wrinkle.

**Copidognathus* (s.s.) *loricifer* M. André. Plymouth Laboratory Tank.

Copidognathus (s.s.) *rhodostigma* Gosse. Duke Rock, Plymouth.

Copidognathus (s.s.) *lamellosus* Lohmann. Duke Rock, Plymouth.

Copidognathus (s.s.) *glyptoderma* Trouessart
Plymouth Laboratory Tank.

Copidognathus (*Copidognathopsis*) *oculatus* (Hodge). Seaton Beach.

Subfamily LOHMANNELLINAE

Lohmannella falcata Hodge. Duke Rock, Plymouth.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

THE SYNONYMIES OF *HALICLONA ANGULATA* (BOWERBANK) AND *H. ARCOFERUS* (VOSMAER)

By Maurice Burton

Ann. Mag. Nat. Hist., Ser. 12, Vol. 1, 1948, pp. 273-84

The classification of sponges must be based on the characters of the spicules, and to a larger extent this is true also of the identification of species. In identification, however, there is a certain unreliability introduced because categories of spicules, particularly of microscleres, may be sufficiently rare that they will be overlooked except in the most thorough microscopic examination. The recognition of this principle and the use of microscopic characters, as well as knowledge of the ecology, has made it possible to sort into two natural groups, corresponding to *H. angulata* and *H. arcoferus*, a long series of specimens formerly assigned to more than a dozen species belonging to different genera.

M.B.

THE ECOLOGY AND NATURAL HISTORY OF *TETHYA AURANTIUM* PALLAS

By Maurice Burton

Ann. Mag. Nat. Hist., Ser. 12, Vol. 1, 1948, pp. 122-30

It is too often found that our knowledge of even the better-known species of sponges is concerned mainly with the external form and the spiculation. Details of exact distribution and ecology are given either too sparingly or omitted altogether. That these, and other details, have a value to the taxonomist is shown in the study of *Tethya aurantium*. There has, for example, been a disposition on the part of some authors to recognize geographical varieties, based mainly on size, but when the measurements of a wide series of individuals are correlated with distribution and ecology such a view is shown to be untenable. A further lack in the details attached to collected specimens has been the record of the date of collection. In the study of development—in this case of the asexual buds—the absence of such data is a great handicap.

M.B.

THE MOLLUSCAN STOMACH

By Alastair Graham

Trans. Roy. Soc. Edin., Vol. LXI, 1949, pp. 737-78

The internal anatomy of the stomach of sixteen species of lamellibranchs and of ten species of prosobranch gastropods is described. The trochids *Monodonta* and *Calliostoma* show a gastric structure which allows close comparison with the lamellibranchs, allowing for the effects of torsion. Within the filibranchs the genera *Glycymeris*, *Ostrea* and *Mytilus* form a series in which the gastric caecum becomes increasingly complex. *Chlamys*, *Pecten* and *Lima*, on the other hand, show a tendency towards reduction of the caecum. In the eulamellibranchs the stomach is similar, whereas in *Nucula* it is reminiscent of the archaic gastropods.

Within the gastropods the stomach becomes simpler in correlation with a macrophagous carnivorous habit and extracellular digestion. A second factor controlling its plan is a forward migration of the oesophageal aperture until in opisthobranchs and pulmonates this adjoins the intestinal opening.

The structure of the polyplacophoran and cephalopod stomach can be shown to agree with those of the lamellibranchs and gastropods.

The steps in the evolution of the crystalline style from the faecal rod found in the style sac of the stomach of protobranchs, rhipidoglossan and lower monotocardian gastropods are discussed.

A.G.

THE GIANT AXONS OF ANNELIDS

By J. A. Colin Nicol

Quart. Rev. Biol., Vol. XXIII, 1948, pp. 291-3

A review is presented of information concerning the giant axons of annelids. The term is a convenient one for certain nerve fibres relatively much larger than others in any given species. They occur in many families of polychaetes, oligochaetes, and possibly archiannelids, and their pattern in these various groups is discussed. Giant axons may be intrasegmental or intersegmental, unicellular or multicellular; in some species they are divided by segmental septa into longitudinal units. Various lines of evidence demonstrate that they are concerned with quick contractions of the entire animal, in both polychaetes and oligochaetes. Measured conduction velocities for these axons are listed, and they are shown to conduct from 2 m. per sec. in *Nereis* up to 45 m. per sec. in *Lumbricus*. Conduction velocity is a function both of axon diameter and of the myelin sheath. Their diversity of structure in different families of polychaetes and oligochaetes indicates that they have arisen independently on several occasions within the Chaetopoda.

J.A.C.N.

BOOK REVIEWS

SEXUAL ENDOCRINOLOGY OF NON-MAMMALIAN VERTEBRATES

L. H. Bretschneider and J. J. Duyvené de Wit

Monographs on the Progress of Research in Holland during the War. Published by Elsevier; Distributors: Cleaver-Hume Press. Price: 15s. net.

This is one of the valuable series of monographs on research performed in the Netherlands during the war. It presents results and conclusions of great interest to endocrinologists and to workers on the lower vertebrates, and demonstrates afresh the vitality and critical importance of the comparative point of view.

The book is divided into four parts. Each can be studied independently, but they are integrated by cross-references and a useful index into a lucid and comprehensive picture. While a cyprinid fish, the bitterling (*Rhodeus amarus*), is the protagonist, there is a large supporting cast of vertebrate species.

The first part describes the use made of growth of the ovipositor in the female bitterling as a quantitative assay object. After sections on technique and chemical specificity, the responses to twenty-eight different steroids are detailed. The time-course of the reaction was characteristic for each substance in a given concentration, and markedly different for the oestrane, pregnane and androstane groups. This property suggested the use of the test for the analysis of extracts of tissues and body fluids both of mammals and of other vertebrate groups. The authors themselves tested a number of these, their most spectacular claim being the presence in human urine of a new hormone, unfortunately unsuitable for pregnancy diagnosis, with effects distinguishable from those of all known steroids. Provisionally called 'luteidin', this substance was reported to be present in the pregnanediol glucuronide complex obtained from pregnancy urine. It must be noted that the bitterling test has been criticized by Van Koersveld (1948¹) as neither regular nor specific enough for more than the qualitative detection of steroids as a group, which act at much lower concentrations than other substances.

The second part presents a far-reaching theory, based on varied evidence, of the sexual functions of the pituitary in the bitterling. This concentration on a single species gives the hypothesis a boldness and sweep that enhance its interest for the general problem of pituitary function. The evidence presented here is sometimes understandably slender—thus successful hypophysectomy is reported only in a single fish. On the basis of this result, and of quantitative studies correlating, with suitable time adjustments, the extent of basophilia in a pituitary zone, the condition of the ovary and the ovipositor response, it is concluded that the steroids mentioned in the first part act indirectly, stimulating

¹ Van Koersveld, E., 1948. *Acta Brevia Neerlandica*, Vol. XVI, Nos. 5-8, pp. 66-9.

the pituitary. This stimulation causes production of corpora lutea in the ovary, which in their turn influence the ovipositor—a signal illustration of the critical importance of hypophysectomy for the analysis of steroid and other hormone effects, particularly on lower vertebrates. (This sequence has been confirmed for other substances by Van Koersveld (1948¹), who notes that all have a narcotic action at higher dosages.) Accounts of the blood-supply, innervation and histological changes in the bitterling pituitary lead to the elaboration of a twofold theory of secretion, embracing 'haemocrinia' and 'neurocrinia'. The most striking factual claims are the passage of a 'colloid', originating in the lobi anterior and intermedius, to the brain via the lobus posterior, and the visibly rich innervation of the lobus anterior, in contrast with its homologue in higher vertebrates (cf. review by Harris, 1948²). A section of this part is devoted to the homology of pituitary lobes in various vertebrate groups, especially teleosts, and to the erection of anatomical types of pituitary. It is interesting to compare this survey with parallel wartime work, experimental and anatomical, on certain of the forms discussed (e.g. Waring, 1940,³ on *Anguilla*; Atwill, 1941,⁴ on anurans; review by Waring, 1942,⁵ on various species).

The third part is an almost classical illustration of the uses of comparative histology. The discovery of 'pre-ovulation corpora lutea' in the bitterling—involving in their formation the destruction of the ovum—and of their connection with ovipositor growth, led the authors and their associates to re-investigate the whole problem of follicular derivatives in forty-five species from six vertebrate groups, including man. This part contains an illustrated account of the histogenesis of the bitterling corpora lutea, a revised classification, arising out of the above survey, of normal and abnormal follicular derivatives, a tabulation of their overlapping distribution throughout the vertebrate groups, and a discussion of their histogenetic and functional significance. The hormone which the bitterling corpora lutea are inferred to produce, and which must, unlike progesterone, affect the ovipositor directly, is given the name 'oviductin'.

The last part describes studies on the sexual cycles in the females of three teleost species, *Rhodeus amarus* itself, *Zoarces viviparus* and *Lebistes reticulatus*, and in both sexes of *Bufo bufo*. It is mainly concerned with changes in the gonad, in behaviour and, in *Rhodeus*, with the ovipositor, but set against the background of pituitary activity. Among a number of interesting observations by the authors and their associates may be mentioned the cyclical nature of oestrus in *Rhodeus* and *Lebistes*, signalized by changes of ovipositor length in the former

¹ Van Koersveld, E., 1948. *Acta Brevia Neerlandica*, Vol. xvi, Nos. 5-8, pp. 66-9.

² Harris, G. W., 1948. *Physiol. Rev.*, Vol. 28 (2), pp. 139-79.

³ Waring, H., 1940. *Proc. Roy. Soc. B*, Vol. 128, pp. 343-53.

⁴ Atwill, W. J., 1941. *Amer. J. Anat.*, Vol. 68, pp. 191-208.

⁵ Waring, H., 1942. *Biol. Rev.*, Vol. 17, pp. 120-50.

and, it is claimed, of posture in the latter; the fact that both of these are influenced by water in which males have been kept, from which the existence of another hormone, 'copulin', is inferred; the even more bizarre fact that ovipositor development in *Rhodeus* depends on the presence of the fresh-water mussels in which the eggs are laid; the unusual follicular derivatives produced in adaptation to viviparity in *Zoarcas* and *Lebistes*; and the endocrine function and response to pituitary hormones of corpora lutea in the hitherto mysterious organ of Bidder in *Bufo*. It is noteworthy that many details in the description of the sexual cycle and spawning behaviour of *Rhodeus amarus* agree very closely with the independent account by Chang (1948)¹ of the same processes in the common Chinese bitterling, *Rhodeus ocellatus*. This final part, in general, completes the biological circle, relating to the lives of particular species the reactions exposed by the preceding analysis.

The book leaves us with, if possible, an increased admiration for a people who could make such a contribution to knowledge in this field, as in so many others, during what the editorial foreword, written on V.E. day, tersely calls 'the five years of German occupation'. In this place it is proper to express the hope that this monograph, mainly concerned with fresh-water forms, will stimulate further research into the sexual endocrinology of marine vertebrates, a difficult enterprise, but one from which so much of both theoretical and practical interest may be expected.

W. M. S. RUSSELL

HYDROBIOLOGIA: ACTA HYDROBIOLOGICA, LIMNOLOGICA ET PROTISTOLOGICA

Published by Dr W. Junk, 13, van Stolkweg, The Hague, 1948, 40 guilders

Hydrobiologia, according to the editors' notice, 'will publish articles embodying original research in the field of Hydrobiology, Limnology and Protistology'. The field included is broad, embracing the 'biology' of marine and fresh-water plants and animals, and their systematics and taxonomy. It is truly an international journal, with editors from the Continent, the United Kingdom, and the United States of America. Two numbers have appeared, the first in August 1948; four numbers are to be published annually. The languages accepted are English, French, German, Italian and Spanish. An examination of the seventeen papers presented in these first two issues shows that fifteen are concerned with fresh-water biology, four with marine botany and phytoplankton, and one with physics (penetration of light in fresh water). Most of the papers are in English. Although authors are recommended to give a short summary in an alternative language, none has done so, and few have given any summary at all. This may not be of value for the taxonomic papers, but it certainly would be for the theoretical and experimental studies. The advance

¹ Chang, H. W., 1948. *Sinensia*, Vol. 19, pp. 12-22.

notice for the second issue is hopelessly garbled. More attention should be directed to correcting errors in English.

Of particular interest to marine biologists are the following papers: 'Contributions to our knowledge of British algae', by F. E. Fritsch; 'Le phyto-plancton estival de la "Costa Brava" catalane en 1946', by Ramón Margalef; 'Die Photosynthese des Phytoplanktons vom Gesichtspunkte der Quantenlehre', by R. Maucha. A new limnological method for the investigation of thin-layered epilithic communities, described by R. Margalef, although designed for freshwater algal deposits, probably could be adapted for marine studies. There are reviews of papers and books dealing with hydrobiology, and obituary notices.

J. A. COLIN NICOL

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